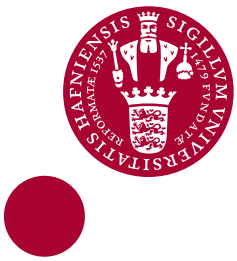

Puppy and adult dog personality

Forkman, Björn; Fält, Lars; Larsson, Ingalil; Olsson, Ann

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Table of Contents

Invited Presentations

- I2 - VOCAL COMMUNICATION IN DOGS - ASPECTS OF INFORMATION CONTENT AND EVOLUTION

Péter Pongrácz* (presenting)

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Abstract:

There are several ways how to investigate dogs' behavior including their acoustic communication. One of the approaches is to consider the main species-specific features of canine behavior as such traits that evolved during the domestication, resulting in a more and more perfect adaptation to the anthropogenic niche. Perhaps the most unique type of vocalization in the dog is barking, which can be found in the closely related Canid species as well; however dogs use it more abundantly and variably than their wild relatives. Our new approach to dogs' bark was based on the assumption that the peculiarities of these vocalizations evolved under the nurturing forces of selection that created such a cluster of signals that convey variable information about the inner state of dogs to a new audience: humans. In a series of playback tests we proved that independently of the amount of their experience with dogs, human listeners can correctly categorize dog barks into several contexts, as well as attribute distinct inner states to the dogs based on the barks. We found that the affective information of dog barks is encoded by the acoustic parameters according to the structural-motivational theory by Morton. Although the acoustic proliferation of dog barks took place since the domestication, we also found evidence that barking may play a role in the intraspecific communication of dogs. In the laboratory as well as at the field, dogs are sensitive to both the contextual and the individual-specific features of other dogs' bark. Another element of the vocal repertoire of dogs is the growl. This conservative vocalization (which in general is identical to the growls of wolves) was investigated in such experiments where we tested whether and how dogs respond to the contextual and indexical information encoded to different types of growls. With the so-called modality matching paradigm we found that dogs emit honest signals regarding their body size in agonistic (food-guarding) context, but their growls convey an exaggerated body size during play. In a recent study we also found that dogs may manipulate the size-related indexical component of their growls when they experience different levels of threat from an approaching stranger. Regarding the contextual information of dog growls, our results showed that dogs differentiate not only between agonistic and playful growls, but also between different agonistic situations, which suggests that dog growls may possess functionally referential attributes, too.
For the future, we propose that the bioacoustical research on dog vocalizations should incorporate more aspects of applied ethology (like animal welfare and the more profound understanding of nuisance barks); as well as conducting surveys on the genetic background of the vocal phenotype of canine vocalizations.

Keywords: *bark; dog; domestication; growl; vocalizations*

Preface

The dog is considered as 'artificial species' by some authors (e.g. Miklósi & Topál, 2013) in a sense that it is a domesticated species without any extant wild-living ancestor – and also almost the entire dog population lives in more or less tight association with humans (i.e. in an 'artificial environment'). Of course, this does not mean that the evolutionary aspects of the behavior of dogs would not be a worthy subject for ethologists – if someone needs to be convinced about this, it is enough to think about the hundreds of empirical and

theoretical papers on dogs' behavior from the last 25 years. The roots of social behavior and cognitive capacity in dogs are originating obviously from its genetic ancestors, however, the long process of domestication (including the challenges of recent and present times) exerted new and strong selective forces on the socio-cognitive traits of dogs as well. This new evolutionary process resulted in such characteristics of dogs that served as adaptations predominantly to the new, anthropogenic environment. Ethologists who are interested in the evolutionary processes as well as in – for example – communicative behavior, find the co-existence between humans and dogs as an especially rewarding research field, because of the easy access to large numbers of experimental subjects of both species, willing to participate in tests, and serving with new and new phenomena to be studied.

Introduction to the research of the acoustic communication of dogs

As it was mentioned earlier, the basic idea behind our scientific approach to dog behavior was the paradigm stating that the most important species-specific feature of dogs is the capacity to get interactively integrated to the anthropogenic environment. This means that the human group represents the natural environment for the dog (e.g. Topál et al., 2009), which needs sophisticated means of adaptations from the dog, enabling it to survive and thrive. Following the concept of 'human behavioral complex' (Csányi, 2000), communication is one of the important ingredients that is essential for successful group living. In case of dog-human co-existence, our main research target was understandably the interspecific communication; however, specific forms of intraspecific signaling provided also interesting contrasts for a better understanding of the complexity of canine vocal behavior.

The importance of acoustic signals in dog-human communication

Similarly to the Canid species living in the wild, dogs communicate also predominantly through the sensory channels of olfaction, vision and hearing. The possible relevance of dog-human acoustic communication emerges from among the other means of information transfer due to the limitations of our species in comprehending canine chemical and visual signals. Canine chemical signals play an important intraspecific role in sexual and individual recognition (Bradshaw & Nott, 1995); however, they may not be relevant for humans, for example because of the difference between the sensitivity of olfactory systems of the two species (Marshall & Moulton, 1981). Dogs' visual signals, although they can be apparent, show strong taxon-specificity. While there is a significant overlap between the visual signals of wolves and dogs (Bradshaw & Nott, 1995), the opposite is true for dogs and humans. It was shown for example that young infants misjudge the emotional state of dogs based on the assessment of dog portraits (Meints et al., 2010). Four-year-olds typically thought that dogs depicted with aggressively exposed teeth were 'happy' – presumably because of the resemblance between human smile and the facial signs of canine aggression. We can assume that most of the visual signals of dogs are hard to interpret correctly for humans without ample experience with them.

Acoustic signals however, may convey the message in a more universal way about the signaler's inner state and particular indexical features. According to the so-called 'motivational-structural (MS) rules' coined by Morton (1977), the inner state of the individual is reflected by the acoustic features of the call that are dependent on the vocal production organs of an individual: harsh (broadband), lower-frequency vocalizations are used in agonistic contexts; tonal, higher-frequency calls in appeasing or non-agonistic contexts. Importantly, these 'rules' seem to apply to a wide range of species (at least among mammals and birds), which make acoustic signaling a likely channel of interspecific communication. According to Morton's theory, in terms of the evolution of competitive signal production, the emission of harsh, low frequency sound is linked to a relatively larger body size. If the receiver responds as expected, such signals may also determine the outcome of an agonistic encounter. Due to their size-dependency, such vocalizations may help to solve confrontations without actual physical interaction in evolutionary terms ('expressive size symbolism', Morton 1994).

The above outlined framework provided a suitable starting point for the investigation of the extent, mechanism and possible evolutionary origins of dog-human acoustic communication.

The information encoded in acoustic signals

Acoustic signals are arguably among the most complex ways of information transfer. Although there are many robust, simple vocalizations used by various species, we should also remember that human language, the most sophisticated natural communication system is also primarily an acoustic one.

Information encoded in the acoustic signals can be sorted into three basic categories (Taylor et al., 2014). Indexical information refers to such attributes of the caller, like body size, sex, age etc. The inner state of the signaler, like hunger, fear, aggression, happiness is transferred as so-called non-referential information (affective communication, graded signals). Finally, when the vocalization denotes an entity of the environment independent of the signaler's inner state, we may consider it as functionally referential information (Marler et al., 1992).

We have already mentioned the structural-motivational theory by Morton (1977) that explains the universality of affective signals with the interconnectedness between certain anatomical features and the likelihood of particular inner states. Another important factor in the evolution of communicative signals is thought to be ritualization (Hinde, 1981). According to this, originally there was a tight connection between certain inner states and the phenotypic phenomenon occurring parallel with them (like vocalizations, postures etc.). During ritualization, this tight connection could be loosened, and the audible (visible etc.) byproduct of the inner state could be intensified, becoming a more obvious signal, already representing the inner state behind. The more independent (and 'cheap') became signals to produce, the possibility for dishonest signaling arose.

Indexical information that encodes the caller's body size is one of the often studied aspects of acoustic communication. Perhaps the best-known theory behind is the independent source-filter theory (Fitch & Hauser, 2003). Briefly, according to this, the quality of sound is predominantly affected by two factors: the 'source', which means the vocal folds in mammals; and the 'filter', that is a more or less intricate 'tube' above the vocal folds, called vocal tract. As the length of the vocal tract is usually in a strong correlation with the body size, the acoustic parameters of a call affected mostly by the 'filter' may also correlate with the size of the body. Formant dispersion is known to be one major parameter of the sound having such indexical relevance (Riede & Fitch, 1999).

Evolutionary changes in the vocal communication of dogs

There are extensive comparative descriptions of the vocal repertoires of dogs, wolves and some other closely related wild Canid species (Cohen & Fox, 1976; Tembrock, 1976). The authors enumerated the vocalization types and the contexts where particular vocalizations seemed to be relevant. One of the rather remarkable outcome of these early efforts was that a certain sort of vocalization, barking, turned out to be almost a 'trademark' for dogs – while the closest relative of dogs, grey wolves bark only in a few (agonistic, resource-holding) contexts, dogs bark in a strongly repetitive manner and in almost each possible contexts. From the ethologist's point of view this discovery represented rather a difficulty than advantage. For decades, it seemed to be almost impossible to find a convincing theory that would explain the evolutionary background of such a hypertrophied way of vocalization in the dog – from the aspect of communication.

If dog barking is considered as a form of communication, the researcher should prove that barks can be characterized with context-specific acoustic features, and most importantly they elicit specific reaction from the receiver. Additionally, we may expect also that according to the biological definition of communication (Scott-Phillips, 2008) the response of the receiver would be advantageous for the signaler (i.e. the barking dog). Only if these requirements are fulfilled would it be plausible considering dog barks as communicative signals. However, for decades researchers did not find any relevantly specific behavioral response in dogs as

a reaction to other dog's barking. It is not surprising therefore that in the late 20th century mostly non-communicative hypotheses existed as explanations of the evolution of abundant barking in dogs. These theories agreed that the barking behavior of dogs is an outcome of changes along (or due to) domestication, but at the same time they did not assign specific communicative function to the barking. For example, according to the 'theory of neoteny', barking is one of the 'neotenic' features of adult dogs, being characteristic at the same time to the juvenile wolves (Schassburger, 1993). Another theory is considering dogs' barking as a general indicator of the state of excitement (Coppinger & Feinstein, 1991), emerging in the lack of strict counter-selective forces since domestication. Other authors consider barks as 'minimally informative vocalizations', referring to the acoustic and functional resemblance between 'contagious barking' among dogs and the well-known phenomenon of mobbing choirs in many other species (Lord et al., 2009).

The research about the communicative function of dog barks gained new momentum, when it was found that there are stable acoustic differences among barks originating from different contexts (Yin, 2002; Yin & McCowan, 2004). Although indirectly, these results indicated that dog barks may show reliably the inner state of the signaler in particular contexts. Similarly important addition was the theory by Feddersen-Petersen (2000) to the theoretical framework of the evolution of dog barks. She hypothesized that while the vocal signals of wolves served predominantly as long-distance communication (howls), the domesticated dog's new social environment included importantly humans also, and new selective forces favored short and mid-distance vocalizations – like barks.

Our approach to the investigation of dog barks was supported by the results and theories mentioned in the previous paragraph, and based on the notion that during the domestication the most relevant selective pressure on dogs shaped their behavior and cognitive capacity towards being compatible with the anthropogenic environment (e.g. Miklósi & Topál, 2013). Therefore in a series of experiments we studied whether barks are informative to the 'new audience' of dogs – humans (Pongrácz et al. 2005, 2006, 2010, 2011; Molnár et al., 2006, 2010). Employing the cutting edge tool park of computerized machine learning technologies, we explored the extent of acoustic information encoding in barks (Molnár et al., 2008; Larrañaga et al., 2015). As a late return to the 'old favorite' of ethologists, we made discoveries regarding the intraspecific communicative function of barks (Maros et al., 2008; Molnár et al., 2009; Pongrácz et al., 2014).

As a counterpart for dog barks in the canine 'vocabulary', another focus of the investigation was laid on growls. This type of vocalization can be regarded as 'conservative' from an evolutionary aspect, as it has a similar occurrence contextually (and acoustically) in wolves and dogs (Cohen & Fox, 1976). Meanwhile the indexical information (regarding the caller's body size) of dog growls was studied in details using human subjects as listeners (e.g. Taylor et al. 2008, 2010), we aimed our efforts to test whether dog growls in different context convey realistic size information of the signaler to the canine audience (Faragó et al., 2010a; Bálint et al., 2013). Besides the indexical information content, another study was performed about the possible referentiality of dog growls emitted in different contexts as well (Faragó et al., 2010b).

Brief review of the results on dogs' acoustic communication

A long series of experiments has been performed about the mechanism and function of different types of dog vocalizations, where we tested the hypotheses about the evolution of intra- and interspecific communication in dogs. This topic has an additional intriguing feature namely that the inter-specific aspect of dogs' communication manifests itself through the interactions with humans; therefore we can also formulate theories about the forces of selection on vocal communication during the domestication process.

It seems likely that different types of dog vocalizations went through somewhat different evolutionary changes during domestication. While growls remained mostly in their 'original' form, dog barks literally proliferated. With the help of our results, based on mainly the

playback experiments where different populations of human listeners were tested with dog bark sequences of particular contexts, now we are able to formulate a well-supported new theory about the evolution and function of dog barks. Besides the newly discovered content of information conveyed about the inner state and identity of the caller towards other dogs as receivers (Maros et al., 2008; Molnár et al., 2009; Pongrácz et al., 2014), dog barks carry plentiful, various and easy-to-decode information for the human audience as well. Importantly, dog barks are 'understandable' for humans without the constraints of extensive learning, as it was found that adults with both ample and minimal dog-related experience (Pongrácz et al., 2005), young children (Pongrácz et al., 2011), and even congenitally sightless people (Molnár et al., 2010) can recognize the contexts of barks with similar success, above chance level. Based on the bark playbacks, human participants attributed inner states to the dogs; feasible in the given contexts of barks as well (e.g. Pongrácz et al., 2005). In a study where we assembled artificial bark sequences based on a pool of original individual bark segments, it was found that human listeners decipher the possible inner states of dogs according to the predictions of the structural-motivational rules by Morton (1977). According to our hypothesis, the contextual 'understanding' of dog barks in humans is based also on the involuntary assignment of particular inner states to dog barks in the 'first step' of mental processing of auditory inputs. Although dogs are sensitive to the auditory cues distinguishing individuals (Maros et al., 2008; Molnár et al., 2009; Pongrácz et al., 2014), and with machine learning algorithms we confirmed that it is possible to discriminate among the barks of individual dogs (Larrañaga et al., 2015), to our present knowledge humans are less adept in telling apart dogs based on the barks (Molnár et al., 2006).

According to our hypothesis about the evolutionary changes in dog barks during domestication (Pongrácz et al., 2010), the first step could be a spontaneous inflation of acoustic variability of barking vocalizations due to relaxed selection in the anthropogenic environment. At the same time, this new environment also raised new challenges (e.g. short or mid-distance signaling to a 'new audience'; new sort of social interactions), which were possible to tackle by means of vocalizations due to the universal rules of acoustic information encoding. Why barks become the most typical form of vocalization in dogs, can be explained by the fact that this type of signal had the opportunity acoustically for changing the most. Unlike the rather long, undivided howls, growls and whines, bark consists of short units, which opens up the possibility of quantitative proliferation as well as through the various lengths of interbark-intervals, it adds another important way how to encode information (Pongrácz et al., 2006). Besides the complexity of segmentation, bark sequences show a spectacular variability of other acoustic parameters as well, like harmonic-to-noise ratio and frequency. Compared to the generally low-pitched, harsh barks of wolves, dog barks radiated to the other extremes (tonal, high-pitched) of acoustic possibilities. This made it possible that while these vocalizations still remained in the category of 'barks', they can be used as vocal phenotypes of other inner states, unlike the purely agonistic barks of wolves. On the theoretical level, it would be a fascinating evolutionary enigma whether a similarly informative communicative system could been evolved in dogs, based on howls, growls or whines instead of barks.

Growls provided an excellent subject for testing other types of information encoded in dog vocalization. By using pre-recorded growls from three contexts (food-guarding, threatening stranger, playing tug-of-war) in an experimental situation, where only one of these was appropriate (food guarding), it was possible to study whether dogs are sensitive to the contextual relevance of different growls (Faragó et al., 2010b). The results of these experiments showed that food-guarding growls discouraged other dogs from taking away a bone more effectively than growls recorded in the other situations. As we found difference between the effect of two agonistic-type of growls (food-guarding and threat-repelling), and not only between agonistic and playful vocalizations, these results provided first evidence of context specificity of agonistic vocalizations in the dog. An ongoing research is aiming to the same question regarding the context specific information of growls, however with human

audience as receivers.
Regarding the indexical information encoded to dog growls, we tested in a modality-matching setup, whether dogs can assess the size of another dog if they hear an agonistic (food-guarding) growl paired with simultaneous projection of two dog pictures (Faragó et al., 2010a). One of the pictures matched the size of the original growling dog, while the other image was either 30% larger or smaller. In control groups, indifferent noise, pictures of cats or projections of geometric shapes were used. The results showed that dogs look sooner and longer at the dog picture matching the size of the growling dog, suggesting that dogs have a correctly sized mental representation of a dog upon hearing its agonistic growls. Although these results indicated that growls convey honest indexical cues about the size of the signaler, the analysis of the acoustic parameters in different growls showed that playful growls have narrower formant dispersion than the agonistic growls of the same dog (Faragó et al., 2010b). As such difference would indicate that dogs are able to send acoustic signals with altered size-information encoded within, a second study was conducted, examining the body size information conveyed by playful growls (Bálint et al., 2013). Again, with the cross-modal matching method, we tested whether dogs prefer to look at the picture of a matching size dog when they were offered two differently sized projected dog-photographs simultaneously with a playback of a growl. Besides confirming the earlier results of Faragó et al. (2010a) regarding the size-accurate information encoded to agonistic growls, we found that dogs looked at rather the larger than the matching size dog when play growls were played back. These results were the first to show that dogs may communicate an exaggerated body size by the means of their growls during play, which may help in maintaining or enhancing the playful interaction. Although acoustic size exaggeration may work as play signal in the case of particular dog vocalizations, a recent study also showed that dogs may be able to 'adjust' their honesty about their size, depending on the level of danger they encountered in an agonistic context. With the 'threatening stranger' method we found that dogs growled differently if they were approached by a man or a woman (Faragó et al., 2016 *in press*). The body size of the 'threatening human' did not have a strong effect on the growls' acoustics, however with careful analysis we could show that the encoded size of signaler is 'larger' in case of a male human opponent than in case of a female. Considering that men represent a stronger threat during an agonistic interaction for a dog than women do, these results could be the first showing that dogs may manipulate their indexical signals according to the need for deterrence in a possible hostile interaction.

Possible new research directions

After almost two decades of research on the information content, function and evolution of dog vocalizations, luckily there are still plenty of unknown areas, offering new challenges for the ethologist. The constant advance in technology allows us to include such strategies and methods that connect behavioral research with cutting edge neurobiology (e.g. Andics et al., 2014; Faragó et al., 2014). There is still a major lack of applied research regarding dog vocalizations, although both from the aspect of animal welfare (e.g. new methods in diagnosing separation-related disorder) and the peaceful coexistence of dog owners and the less dog enthusiastic part of the society (e.g. nuisance barks – Pongrácz et al., 2016 in press) it would be time for the employment of some of the empirical results on canine acoustic communication.

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References

Andics, A., Gácsi, M., Faragó, T., Kis, A., Miklósi, Á., 2014. Voice-sensitive regions in the dog and human brain are revealed by comparative fMRI. Current Biology 24, 574-578.

Bálint, A., Faragó, T., Dóka, A., Miklósi, Á., Pongrácz, P., 2013. 'Beware, I am big and non-dangerous!'–Playfully growling dogs are perceived larger than their actual size by their canine audience. Applied Animal Behaviour Science 148, 128-137.

Bradshaw, J.W.S., Nott, H.M.R., 1995. Social and communication behaviour of companion dogs. In: Serpell, J. (Ed.) The Domestic Dog – Its Evolution, Behaviour and Interactions with People. Cambridge University Press, Cambridge, UK, 115-130.

Cohen, J.A., Fox, M.W., 1976. Vocalizations in wild canids and possible effects of domestication. Behavioural Processes 1, 77-92.

Coppinger, R., Feinstein, M., 1991. Hark! Hark! The dogs do bark. . . A new theory on why dogs bark. Smithsonian 21, 119-128.

Csányi, V., 2000. The 'human behaviour complex' and the compulsion of communication: Key factors of human evolution. Semiotica 128, 45-60.

Faragó, T., Pongrácz, P., Miklósi, Á., Huber, L., Virányi, Zs., Range, F., 2010a. Dogs' expectation about signalers' body size by virtue of their growls. PLOS One 5(12), e15175.

Faragó, T., Pongrácz, P., Range, F., Virányi, Zs., Miklósi, Á., 2010b. 'The bone is mine': affective and referential aspects of dog growls. Animal Behaviour 79, 917-925.

Faragó, T., Andics, A., Devecseri, V., Kis, A., Gácsi, M., Miklósi, Á., 2014. Humans rely on the same rules to assess emotional valence and intensity in conspecific and dog vocalizations. Biology Letters 10, 20130926.

Faragó, T., Bálint, A., Miklósi, Á., Pongrácz, P., 2016. Threat level dependent manipulation of signaled body size – dog growls' indexical cues depend on the different levels of potential danger. Animal Cognition (in press).

Feddersen-Petersen, D.U., 2000. Vocalisation of European wolves (Canis lupus lupus L.) and various dog breeds (Canis lupus f. familiaris). Archiv für Tierzucht 43, 387-397.

Fitch, W.T., Hauser, M.D., 2003. Unpacking honesty: vertebrate vocal production and the evolution of acoustic signals. In: Simmons, A.M., Popper, A.N., Fay, R.R. (Eds.), Acoustic Communication. Springer, New York, 65-137.

Hinde, R.A., 1981. Animal signals: Ethological and games-theory approaches are not incompatible. Animal Behaviour 29, 535-542.

Larrañaga, A., Bielza, C., Pongrácz, P., Faragó, T., Bálint, A., Larrañaga, P., 2015. Comparing supervised learning methods for classifying sex, age, context and individual Mudi dogs from barking. Animal Cognition 18, 405-421.

Lord, K., Feinstein, M., Coppinger, R., 2009. Barking and mobbing. Behavioural Processes 81, 358-368.

Marler, P., Evans, C.S., Hauser, M.D., 1992. Animal signals: motivational, referential, or both. In: Papousek, H., Jürgens, U., Papousek, M. (Eds.) Nonverbal Vocal Communication: Comparative and Developmental Approaches. Cambridge University Press, Cambridge, UK, 66-86.

Maros, K., Pongrácz, P., Bárdos, Gy., Molnár, Cs., Faragó, T., Miklósi, Á., 2008. Dogs can discriminate barks from different situations. Applied Animal Behaviour Science 114, 159-167.

Marshall, D.A., Moulton, D.G., 1981. Olfactory sensitivity to α-ionone in humans and dogs. Chemical Senses 6, 53-61.

Meints, K., Racca, A., Hickey, N., 2010. Child-dog misunderstandings: children misinterpret dogs' facial expressions. In: Proceedings of the 2nd Canine Science Forum, Vienna, Austria, 99.

Miklósi, Á., Topál, J., 2013. What does it take to become 'best friends'? Evolutionary changes in canine social competence. Trends in Cognitive Sciences 17, 287-294.

Molnár, Cs., Pongrácz, P., Dóka, A., Miklósi, Á., 2006. Can humans discriminate between dogs

on the base of the acoustic parameters of barks? Behavioural Processes 73, 76-83.

Molnár, Cs., Kaplan, F., Roy, P., Pachet, F., Pongrácz, P., Dóka, A., Miklósi, Á., 2008. Classification of dog barks: a machine learning approach. Animal Cognition 11, 389-400.

Molnár, Cs., Pongrácz, P., Faragó, T., Dóka, A., Miklósi, Á., 2009. Dogs discriminate between barks: The effect of context and identity of the caller. Behavioural Processes 82, 198-201.

Molnár, Cs., Pongrácz, P., Miklósi, Á., 2010. Seeing with ears: Sightless humans' perception of dog bark provides a test for structural rules in vocal communication. The Quarterly Journal of Experimental Psychology 63, 1004-1013.

Morton, E.S., 1977. On the occurrence and significance of motivationstructural rules in some bird and mammal sounds. American Naturalist 111, 855-869.

Morton E.S., 1994. Sound symbolism and its role in non-human vertebrate communication. In: Hinton, L., Nichols, J., Ohala, J.J. (Eds.), Sound Symbolism. Cambridge University Press, Cambridge, MA, 348-365.

Pongrácz, P., Miklósi, Á., Molnár, Cs., Csányi, V., 2005. Human listeners are able to classify dog barks recorded in different situations. Journal of Comparative Psychology 119, 136-144.

Pongrácz, P., Molnár, Cs., Miklósi, Á., 2006. Acoustic parameters of dog barks carry emotional information for humans. Applied Animal Behaviour Science 100, 228-240.

Pongrácz, P., Molnár, Cs., Miklósi, Á., 2010. Barking in family dogs: An ethological approach. The Veterinary Journal 183, 141-147.

Pongrácz, P., Molnár, Cs., Dóka, A., Miklósi, Á., 2011. Do children understand man's best friend? Classification of dog barks by pre-adolescents and adults. Applied Animal Behaviour Science 135, 95-102.

Pongrácz, P., Szabó, É., Kis, A., Péter, A., Miklósi, Á., 2014. More than noise?—Field investigations of intraspecific acoustic communication in dogs (Canis familiaris). Applied Animal Behaviour Science 159, 62-68.

Pongrácz, P., Czinege, N., Haynes, T.M.P., Tokumaru, R.S., Miklósi, Á., Faragó, T., 2016. The communicative relevance of auditory nuisance – barks that are connected to negative inner states in dogs can predict annoyance level in humans. Interaction Studies (in press).

Riede, T., Fitch, W.T., 1999. Vocal tract length and acoustics of vocalization in the domestic dog (Canis familiaris). Journal of Experimental Biology 202, 2859–2867.

Schassburger, R.M., 1993. Vocal communication in the timber wolf, Canis lupus, Linnaeus: structure, motivation, and ontogeny. In: Advances in Ethology, vol. 30. Paul Parey Scientific Publishers, Berlin, Germany.

Scott-Phillips, T.C., 2008. Defining biological communication. Journal of Evolutionary Biology 21, 387-395.

Taylor, A.M., Reby, D., McComb, K., 2008. Human listeners attend to size information in domestic dog growls. Journal of the Acoustic Society of America 123, 2903-2909.

Taylor, A.M., Reby, D., McComb, K., 2010. Size communication in domestic dog, Canis familiaris, growls. Animal Behaviour 79, 205-210.

Taylor, A.M., Ratcliffe, V.F., McComb, K., Reby, D., 2014. Auditory communication in domestic dogs: vocal signalling in an extended social environment of a companion animal. In: Kaminski, J., Marshall-Pescini, S. (Eds.), The Social Dog – Behaviour and Cognition. Elsevier, Oxford, UK, 131-164.

Tembrock, G., 1976. Canid vocalisations. Behavioural Processes 1, 57-75.

Topál, J., Miklósi, Á., Gácsi, M., Dóka, A., Pongrácz, P., Kubinyi, E., Virányi Zs., Csányi, V., 2009. The dog as a model for understanding human social behavior. Advances in the Study of Animal Behaviour 39, 71-116.

Yin, S., 2002. A new perspective on barking in dogs (Canis familiaris). Journal of Comparative Psychology 116, 189-193.

Yin, S., McCowan, B., 2004. Barking in domestic dogs: context specificity and individual identification. Animal Behaviour 68, 343-355.

- I3 - IS DOG DOMESTICATION REALLY ALL ABOUT HUMANS?

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Domestic dogs live in a human-dominated niche that represents the dog's natural environment. Several researchers have proposed that dogs have been selected to cooperate and communicate with humans during domestication and, thus, evolved some genetic predispositions allowing them to develop skills shared with humans (Hare et al., 2002; Topál et al., 2009; Miklósi & Topál, 2013).
Building on this idea of convergent evolution of dogs and humans, it has been argued that dogs might be an additional, and in some respects, a more informative model when investigating the evolution of human social behavior and cognition than non-human primates (Miklósi et al., 2004; Hare & Tomasello, 2005; Fitch et al., 2010). During the domestication process however, dogs did not only start to interact with humans but began also to explore a new feeding niche by exploiting resources created by human refuse. This change in feeding ecology -from being a primary cooperative hunter to a scavenger- and subsequent changes in social structure -from cooperative breeding to a promiscuous system with a significant reduction in allomaternal care- likely also affected dogs' cognitive skills and tolerance.
In this talk, we will first discuss basic motivational differences (e.g. exploration/persistence) between wolves and dogs likely linked to their respective feeding ecology (hunting vs. scavenging). Second, by presenting experiments on intraspecific tolerance and cooperation, we suggest that results on both these aspects are easily explained by differences in the social behaviors of the two species (i.e. reduced reliance on cooperative activities in both the reproductive and foraging context). Finally, we will critically re-evaluate results from studies looking at wolves' and dogs' interactions with humans taking into account the observed differences in both motivational aspects and intraspecific social behaviors.
In conclusion we will argue that, when investigating the effects of domestication, it is important to regard the domestic dog not 'just' as humans' best friend, but rather consider dogs as a species adapted to a complex ecology characterized by feeding conditions and social organizations that are different from those of wolves not only in relation to humans. Importantly, we do not deny the role of human selection on dog behavior, but rather promote a wider view of dog domestication, which will help us to design tests and behavioral analyses that are better suited to dissect possible functions and underlying mechanisms of dog behavior.

References

Fitch, W.T., Huber, L., Bugnyar, T., 2010. Social Cognition and the Evolution of Language: Constructing Cognitive Phylogenies. Neuron 65, 795-814.

Hare, B., Brown, M., Williamson, C., Tomasello, M., 2002. The domestication of social cognition in dogs. Science 298, 1634-1636.

Hare, B., Tomasello, M., 2005. Human-like social skills in dogs? Trends in Cognitive Sciences 9, 439-444.

Miklósi, Á., Topál, J., 2013. What does it take to become 'best friends'? Evolutionary changes in canine social competence. Trends in Cognitive Sciences 17, 287-294.

Miklósi, A., Topal, J., Csanyi, V., 2004. Comparative social cognition: what can dogs teach us?

Animal Behaviour 67, 995-1004.

Topál, J., Gergely, G., Erdöhegyi, Á., Csibra, G., Miklósi, Á., 2009. Differential Sensitivity to Human Communication in Dogs, Wolves, and Human Infants. Science 325, 1269-1272.

- I4 - CANINE COGNITION IN COMPARATIVE CONTEXT

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Abstract:

To put dog cognition into an appropriate comparative context, we have to consider what a dog is. Dogs can usefully be characterized in three ways: phylogenetically, as carnivorans and specifically canids; ecologically, as social, cursorial hunters; and anthropocentrically, as domestic animals. A principled comparative understanding of canine cognition should therefore involve comparing dogs' cognition with that of other carnivorans, other social hunters, and other domestic animals. For the first and third of these categories, we know substantially more about dog cognition that of most or all of the other species in them; among the other social hunters, however, we have two taxonomic groups (chimpanzees and bonobos, and the bottlenose dolphins) whose cognition has been well studied; and domestic animals include one very well studied species, the pigeon. The presentation therefore compares dog cognition with what is known about cognition in species that fit into these categories, with a particular emphasis on wolves, cats, spotted hyenas, chimpanzees, dolphins and pigeons. Several categories of cognition are covered, including sensory cognition, motor skill, physical cognition, spatial cognition, social cognition, and self-awareness. Although the comparisons are incomplete in several ways, it does appear that dogs' cognition is influenced by their membership of all three of these groups, and taking all three groups into account, dog cognition does not look exceptional. The great increase in the study of dog cognition in the current century has contributed to comparative cognition in many ways, but two stand out. First, it has demonstrated the importance of social interaction with humans and conspecifics in the performance of cognitive tasks. More generally, it has provided a well-understood standard, with which the cognition of other species, related in one way or another to dogs, can be intelligently compared. Such comparisons would extend our understanding of cognition in dogs as well as in the other species concerned. It would be particularly useful to apply such comparisons to two groups that have not been formally studied to any great extent, domestic equids and tamed raptors.

Keywords: *dog; cognition; carnivoran; social hunting; domestic animal*

Canine cognition in comparative context

I start with two apologies. The first is that, unlike almost everyone else contributing to this Forum and this volume, I am not an expert on dogs. True, I have published a paper or two on dog cognition; and (this time like everyone else, I am sure) I have got the makings of one or two more in my files somewhere, if only I could find the time and effort to write them up. But most of my research in animal cognition has been in other species.

So what am I doing here, and what have I got to tell this audience? Oddly, the answer is the same as my opening apology: I am not an expert on dogs. In fact, after nearly five years of editing the journal *Animal Cognition*, I have come to doubt whether I am an expert on any species at all. What I do have, partly as a result of that editing experience, and partly because of an advanced course I have been teaching during roughly the same period, is an overview, perhaps a wider overview than most people, of the broad field of animal cognition, across a wide sweep of taxa. So what I am doing here is to try to put one very important aspect of modern canine science, namely dog cognition, into a comparative context.

But this leads on to my second apology. The task of truly setting canine cognition into its comparative context turns out to be a huge one. The present paper is therefore a report of a work in progress. It is based on the literature I have read and noted during recent years of editing the journal and teaching, rather than on the systematic scouring of the book and journal literature that I am ultimately planning… but which seems likely to take me several times the time I had from being invited to give this paper to actually giving it, even if I hadn't had a few other things to do at the same time. Nor have I made full use of some recent reviews of dog cognition, e.g. Miklósi (2014) and Bensky et al., (2013), partly because my aim is slightly different from theirs. For all these reasons, this is a first look; it will doubtless contain gaps and errors, and I shall be very pleased to have those pointed out; but I hope it will serve to set an agenda, even if not to report complete conclusions.

So, how should we approach the task of truly setting canine cognition into its comparative context? More precisely, what other species should we compare dogs and their cognition with? All and any of them? That would be an impossible task; even among the vertebrates, there are over 5000 other species of mammal, over 8000 species of bird, about 28000 species of teleost fish, and numerous members of other classes to consider; and then there are the uncountable numbers of invertebrate species. The same iron law of large numbers means that taking a random selection of other species into a comparison would be irrational to the point of absurdity – yet that is what we would find ourselves doing if we simply looked up the species "dog" in the index of one of the great texts on animal cognition, such as Mackintosh's (1974) study of animal learning, or Shettleworth's (2010) study of animal cognition in the context of behavior and its evolution. Why should we compare dog cognition with the cognition of pigeons, rats, or rhesus monkeys, as we would have to if we were using Mackintosh's book; or with the behavior of chickadees, voles and chimpanzees, as Shettleworth's book would allow us to?

The title of the present paper follows from considerations like these. To decide what comparisons we should meaningfully make, we need to answer the question posed by Coppinger and Coppinger (2016) in the title of their recent book: What is a dog? How does this species we are all interested in relate to other species that have been studied (or that need to be studied)? What are the similarities and differences between them – and do they explain the similarities and differences between cognition as we see it in dogs, and cognition as we see it in other species? And, following on from that understanding, what is the unique contribution that the study of canine cognition can make to the study of comparative cognition in general?

I want to pose this key question, what is a dog, in three different ways: phylogenetically, ecologically, and anthropocentrically. That is to say, I want to ask what a dog is in terms of where it fits in to the great tree of descent from different and simpler organisms; what it is in terms of where it fits in to the complex web of resource-driven relationships that link all living things together in a system that is usually close to an equilibrium; and what it is in terms of its role in human history, and humans' role in its history. I will of course be asking all those questions primarily about cognition, though some non-cognitive matters will no doubt find their way in also. And I will be asking them about cognition as such, rather than about the neural mechanisms that subserve it, because I am not a neuroscientist and I am too old to start pretending I am one.

What is a dog, phylogenetically?

From a phylogenetic perspective, dogs are members of the mammalian order Carnivora. I will refer to them as being carnivorans, because the obvious word "carnivore" is ambiguous. Although the order Carnivora gets its name from the fact that, unlike all other mammalian orders, most of its members eat animal flesh, there are a few carnivorans that are not carnivores in this more general sense, and of course many carnivores that are not carnivorans.

Depending who you read, there are currently between 250 and 300 recognized species of carnivorans. The order is divided into two suborders, the cat-like feliforms and the dog-like

caniforms. Each has several families within it: as well as the felids, the feliforms include civets, linsangs, hyenas and mongooses, while the caniforms include bears, seals and sea lions, the red panda, skunks, mustelids and raccoons. But despite the number of other carnivoran species, the world population of dogs, estimated at 400 to 1200 million (Coppinger & Coppinger, 2016) comfortably exceeds that of all other carnivorans combined except the domestic cat (perhaps 600 million).

In seeking to place dog cognition into its phylogenetic context, therefore, we would like to be able to see how far the cognition of dogs is similar to, and different from, that of the other 250+ members of the order. But this ideal program faces a snag. Just as the world population of dogs comfortably exceeds that of almost all other carnivorans combined, so too the world literature on dog cognition comfortably exceeds that on the cognition of all other carnivorans. I am basing the present paper on the current contents of my personal data base, which of course is far from complete, but is likely to be representative. At the moment when I started writing this paper, I had indexed 508 papers under "dog cognition" or subheadings within it in my personal data base. I only had 70 more for cognition in the whole of the rest of the carnivorans. In other words, our knowledge of carnivoran cognition derives very largely from studies on dogs. This time there is no real exception for cats, though they do run into second place, especially if we take into account literature whose primary purpose was to investigate brain mechanisms – compared with dogs, cats have rather regular brains so they are more promising subjects for neurophysiological investigation. There is also a significant literature on brain-damaged ferrets. But I don't like that kind of literature, and I find it difficult to extract the true cognitive content from it, so for the time being I am not going there at all.

In part this focus on dogs within the literature of carnivoran cognition reflects the long history of the use of dogs as "model organisms" in biomedical research, as a result of which they found their way into various kinds of psychological investigation. The most famous example, of course, was Pavlov's (1927) foundational work on salivary conditioning, which expanded into an entire school of investigation in the Soviet Union and, between 1945 and 1990, the Soviet satellite states in Eastern and Central Europe (see Wyrwicka, 1994). But dogs were also put to use in the "model organism" phase of Western comparative psychology, for example in avoidance learning experiments (e.g. Solomon & Wynne, 1953; Brush et al., 1955). This kind of research was, by modern standards, the very reverse of comparative, in that it did not allow for meaningful comparisons between species that there was any a priori reason to compare. However, it does contribute to our body of knowledge; and, apart from a few studies of cats (including some of the very earliest work in comparative psychology, e.g. Thorndike 1898) and of raccoons (for which see Pettit, 2010), what we learned about carnivoran cognition in that period was almost entirely about dog cognition.

There is also a much more creditable reason for the dominance of dog literature within comparative cognition, however, and that is the upwelling of work on dog cognition in the present century, much of it led by colleagues who are represented here at this forum, either directly or through their students and associates. We will be coming to some of their work later in this paper.

Given this predominance of dog studies within carnivoran cognition, it is not surprising that there are quite a few fields of cognition in which we know a fair amount about dogs but nothing, or next to nothing, about other carnivorans, so locating those aspects of dog cognition within carnivoran cognition is impossible. However, as we shall see, it is possible to identify a number of fields of cognition in which we have significant evidence both about dogs and about one or more other species of carnivorans. It is also possible to identify some fields in which we have knowledge about some other carnivorans and few or no comparable studies have been dogs; these represent obvious research possibilities for the growing army of dog cognition researchers.

What is a dog, ecologically?

To understand what a dog is ecologically, we have to turn to their wild ancestor, the grey wolf *Canis lupus*. At least on the biological species concept of Mayr (1942), there is no doubt that dogs are conspecific with wolves, in that the two populations hybridize freely and the hybrids are fertile – though it has to be remembered that this is true across a wide range of the genus *Canis*. Ecologically speaking, the grey wolf is an unusual caniform, and even an unusual member of its genus: although it is, like most carnivorans, carnivorous, and like most canids, a hunter rather than a sit-and-wait predator, it is unusual in being gregarious, hunting in packs, and feeding principally on animals larger than itself. Put briefly, wolves are social cursorial hunters.

What other animals share this way of making a living? Social hunting within the Carnivora has been valuably reviewed by Bailey et al. (2013), who consider a wide range of possible examples; here I will focus only on the most salient. Certainly some of the other closely related canids, such as the red wolf and coyote, do also hunt socially, and take prey larger than themselves. But they do so only occasionally, and there is little to suggest that they often, if ever, engage in the lengthy pursuits of prey that characterize wolves' hunting (Bekoff, 1977; McVey et al., 2013). The closest in behavior to the grey wolf are the dhole of Asia and the African wild dog, both of which routinely hunt in packs and take prey larger than themselves (Hayward et al., 2006, 2014). Among the large feliforms, the closest in behavior to the wolf is the spotted hyena, which hunts large prey socially (Hayward, 2006); among the felids, only lions hunt socially, and they are not cursorial predators in the same way as wolves, using ambush tactics (Stander, 1992). Most other feliforms take prey substantially smaller than themselves.

What about non-carnivoran carnivores? The animal from another order most closely resembling a wolf was the thylacine, or marsupial wolf, but that unfortunately became extinct before its behavior could be properly studied; however biomechanical examination leads to the conclusion that though it may have hunted in small social groups, like extant carnivorous marsupials it mainly ate prey much smaller than itself (Attard et al., 2011; Figuerido & Janis, 2011). Among other mammalian orders the obvious examples of social cursorial hunters are some of the toothed whales, with the bottlenose dolphins having been well studied; although they do not take prey larger than themselves, they do use well-organized group hunts to attack large shoals of fish (e.g. Gazda et al., 2005). However the most significant case for our purposes may be the chimpanzee. Although meat forms only a small portion of its diet, its targets are often of comparable size if not quite as large as the chimpanzees themselves, e.g. colobus monkeys. Furthermore, meat is typically obtained through group hunting (e.g. Teleki, 1973; Stanford et al., 1994), a behavior which may be unique among apes; even the closely related bonobo, which does also include some meat in its diet, has been thought to target only much smaller animals (Ihobe, 1992, 1997). However the difference between chimpanzees and bonobos may be a function of regional variation in meat-eating, which is substantial for both species (Hofreiter et al., 2010), and some bonobos do eat at least smaller monkeys (Surbeck & Hohmann, 2008).

As regards the other vertebrate classes, group hunting of any sort is rare in birds, though it has been documented for Harris hawks (Bednarz, 1988). Hector (1986) summarizes literature showing that hunting in groups is not uncommon among raptors, but that mostly it is not truly social in that there is no sign of co-operation, and success rates are no higher, and prey sizes no greater, than in solitary hunting. However he collects a number of reports of true co-operative hunting, though mainly between pairs rather than larger groups; Hector's own study of the Aplomado falcon is an example. As yet I have not been able to trace any literature on co-operative pursuit in cold-blooded vertebrates, or indeed in invertebrates, though it would be surprising if there were none. Many species of shark, for example, hunt in groups, but in these cases there seems to be competition rather than co-operation between the group members (e.g. Hobson, 1963; Robbins & Renaud, 2016).

In summary, although we have not found as many other cursorial social hunters as we found other carnivorans, from the point of view of a comparative approach to dog cognition, the ecological comparison set looks rather more promising than the phylogenetic one. It includes at least two very well studied species, the chimpanzee and the bottlenose dolphin, and one, the spotted hyena, for which we have quite substantial information albeit mostly from a single extended research program (Holekamp et al, 2007).

What is a dog, anthropocentrically?

My final way of defining a dog is anthropocentrically. That is to say, the dog is a domesticated animal, so it makes sense to compare it with other domesticated animals. Of course, different animals are domesticated for different purposes, and we might well ask what we could expect dogs to have in common, cognitively or in any other way, with species like pigs that are kept for meat, horses that are kept for physical work, cows and sheep that are kept to allow their bodily products to be harvested, and cats and birds that are kept for aesthetic reasons or companionship. However, all these species are actually kept for more than the purposes I have indicated, and dogs are or have been kept for all of them, to greater or lesser extents. And certainly the purposes for which most dogs are kept nowadays are different from those for which they were first domesticated, or for which they were kept for most of the 14000 to 40000 years since.

Despite the differences, all domestic animals do have some points in common. An increased tolerance for the close presence of humans and indeed of other animals, both conspecifics and others, is one. Individuals of entirely wild species can acquire such tameness, especially if they live with humans from birth, but there is at least some evidence that species that have been long bred in captivity acquire it more quickly and fully than wild conspecifics, a point that will become relevant when we turn to the cognitive comparison of dogs and wolves. Reduced dependence on active foraging for food is another common characteristic of domestic animals, and with it almost certainly increased tolerance of variations from the ancestral diet and of unusual ways of acquiring food – the last a fact that can be useful in devising cognitive experiments. And finally, we should remember that virtually all domestic animals have been subject to deliberate artificial selection (as well as natural selection for the traits we have just listed), for all sorts of traits some of which may have consequences for their cognition or at least for the performance of the tasks by which we seek to evaluate cognition.

There is no need to list all the domesticated animals, but we should note a few that are perhaps less obvious, or whose value for comparison with dogs might be missed. Among the less obvious cases is one that is anomalous but particularly interesting, namely the taming of raptors for falconry. I refer to this as "taming" rather than "domestication" because until very recently all raptors used in falconry were captured from the wild as chicks (Gallagher, 2008). The case is interesting because falcons like dogs are used by humans in co-operative hunting. Another less obvious case is the pigeon; the widespread presence of feral pigeons perhaps leads us to forget that pigeons have a longer history of domestication than any other bird except the chicken, both having been domesticated something between 5000 and 10000 years ago (Johnston, 1992; West and Zhou, 1988) – although Neanderthal humans were eating the pigeon's wild ancestors in substantial numbers thousands of years earlier (Blasco et al., 2014). And of course we should not forget the cat, which we have already identified as a useful comparison species as a carnivoran. Asian elephants form a borderline case; I have not included them as a domestic species here, though arguably one could.

The domestic animals thus afford a number of interesting cases for cognitive comparison with dogs. In addition to cats, which we had noted for phylogenetic reasons, there are good reasons for looking at falcons (as animals used for hunting), horses (as animals commonly submitted to elaborate training), pigeons (as subjects in a huge number of cognitive experiments).

The comparative project

A principled project for setting dog cognition into its comparative context, therefore, might include a determined attempt to compare dogs with the following species, on all of which at least some cognitive literature is available:

- Wolves, as the wild ancestor, and closely related members of the genus *Canis;*
- African wild dogs and spotted hyenas, as both carnivorans and social hunters;
- Cats, both as carnivorans and as domestic animals;
- Falcons, as social hunters and domestic animals (both to a limited extent);
- Bottlenose dolphins and chimpanzees, as social hunters;
- Horses and pigeons, as domestic animals.

A miscellany of other carnivorans, social hunters, and domestic animals can be included opportunistically, where relevant literature is available. It is worth noting some taxa that do not appear on this list. There is no obvious reason to compare the cognition of dogs with that of, say, primates in general, corvids, parrots, rats, bats, cleaner fish, bees, or jumping spiders – interesting as all those animals, and their cognition, are.

There is one other species that we must bear in mind: humans. While we are not carnivorans, we match dogs in that ancestrally, and indeed for the majority of our existence as a species, we were social hunters. And while it may be stretching matters to describe humans as domesticated ("The wildest hath not such a heart as you" – *A Midsummer Night's Dream*, Act 2, Scene 1), we are the context within which the dog has come to differ from the wolf. Furthermore a number of the tasks that we shall be considering in relation to dogs were first devised for testing humans – often young humans. One of the basic reasons for being interested in animal cognition is to understand the uniqueness of human cognition better; and as part of that project, there is a lot more point in comparing human cognition with the cognition of dogs than with the cognition of, say, pigeons – and I write as someone who has been quite heavily involved in doing the latter (e.g. Wills et al., 2009; Maes et al., 2016).

At this point, it would be good to present a table of types of cognition and cognitive tasks within them, comparing the results available from dogs with those from the other taxa we have identified. I am some way off being able to do that. Furthermore, whereas for some of the comparison species, we could usefully sweep in everything that is known about their cognition, for others – especially chimpanzees and pigeons – we can only pick out the most salient points from a vast literature. What follows, therefore, is a set of notes towards such a table, considering some major fields of cognition in turn. Not all fields of cognition are considered here: in particular, I have left to one side studies of abstract reasoning, number, and time sensitivity; and I have not considered memory as a separate category, although it does of course enter into studies of many kinds of cognition.

Associative learning

An obvious place to start is with what are thought of as the simplest kinds of learning. However, we need say very little about them. The basic forms of associative learning – habituation, Pavlovian conditioning, operant conditioning, and avoidance learning – have all been investigated thoroughly in dogs – operant conditioning less thoroughly than the others in the laboratory, but extensively in the applied context of training working and show dogs. No other carnivorans has been investigated as thoroughly in any of them, but from the limited evidence to hand (e.g. on avoidance conditioning in cats, e.g. McAdam, 1964; Seward & Humphrey, 1967) we can reasonably conclude that, so far as we yet know, both dogs and other carnivorans show these simple forms of learning in the same way as other vertebrate species. The same is true of the other social hunters we identified, and of other domestic species: indeed, the pigeon is as stereotypically identified with operant conditioning as the dog is with classical conditioning. That is not to say that the details are the same for all species. It is well accepted that the so called "laws of learning", applying especially to what is usually called conditioning, show species-specific variations at least in their parameters

(Hinde & Stevenson-Hinde, 1973), and dogs are no exception: for example Jenkins et al. (1978) showed that dogs had a "prepared" (in the sense of Seligman, 1970) association between food and licking. But such variations in preparedness are found throughout the animal kingdom.

Sensory cognition

The other foundational way of looking at animal cognition is to start with the stimulus input, and consider what perceptual resources an animal has, and what it is able to do to extract information from the perceptual input. Here there seems more likelihood of finding something distinctive about dogs, because the olfactory capacities of dogs are remarkable, extending to discriminating the direction in which a scent trail has been laid (Wells & Hepper, 2003), and between any two human individuals even, under at least some conditions, monozygotic twins (Kalmus, 1955; Hepper, 1988; Pinc et al., 2011). That is not to say that dogs are always dominated by olfactory information, however: human points can dominate olfactory cues in some situations (Szetei, et al., 2003).

Unfortunately, I have not been able to find anything like comparable tests of olfactory ability with any other carnivoran, or social hunter, or domestic animal; but we do have comparative anatomical data, showing that large canids, including the wolf, have disproportionately large olfactory turbinal surface areas (the nasal structures that allow olfaction) compared with most other carnivorans, except for other large, high latitude carnivores such as the polar bear (Green et al., 2012); conversely, marine carnivorans (i.e. pinnipeds) have much lower olfactory turbinal surface areas (Van Valkenburgh et al., 2011). So the olfactory performance of dogs is probably exceptional as well as being extraordinary.

In taste, dogs outperform cats, in that cats and indeed all felids tested seem to be entirely insensitive to sweet taste for genetic reasons, while dogs have a different genetic structure in the relevant area and do respond to sweetness (Li et al., 2006, 2009); since the ultimate reason for cats' neglect of sweetness is claimed to be their obligate carnivory, it is likely that dogs also outperform many other carnivorans of which the same would be true, though probably not the omnivorous carnivorans such as badgers. There are other sensory modalities where dogs may be less sensitive than some other carnivorans, for example the whisker sense, which seems to be particularly important in aquatic carnivorans and has been well studied in seals (see Hyvarinen et al., 2009); but unfortunately I have not found comparable data on dogs.

The fields of basic visual and auditory perception are too vast to attempt to summarize here, but I am not aware of anything to suggest that dogs are exceptional among carnivorans, either positively or negatively, in either modality at the basic perceptual or psychophysical level. More interesting, in any case, is what animals can do with the sensory input. Although the field of sensory cognition is not particularly well developed for any carnivoran, we do know that dogs can discriminate visual patterns in the same way as has been shown more fully for pigeons, primate species, and some domestic animals; a commonly used discrimination of this kind is between the faces of individual humans, though many other pattern types have been tested (for examples see Racca et al., 2010 and Somppi et al. 2016 for dogs; Troje et al., 1999, for pigeons; Parr et al., 2000, Martin-Malivel & Okada, 2007, for chimpanzees; Kendrick et al., 1995, 2001). There is less evidence for other carnivorans, but some: for example Fields (1936) gave a simple demonstration of visual object discrimination in cats, and black bears have been trained to make both perceptual and more abstract category discriminations (Vonk et al., 2012; Vonk & Johnson-Ulrich, 2014).

Dogs have also been exposed to some of the other widely used tests of visual cognition, for example with occluded or hierarchical stimuli, in which pigeons are often found to behave differently from humans (Sekuler et al., 1996; Cavoto & Cook, 2001); dogs, on the other hand, behave a little more like humans (Pattison et al 2010; Pitteri et al, 2014), as do chimpanzees on the occluded stimulus task (Sato et al., 1997) though only in some experiments with hierarchical stimuli (contrast Hopkins & Washburn, 2002, with Fagot & Tomonaga, 1999).

Among other social hunters, dolphins have been shown to behave like humans in an echolocation analogue of the hierarchical stimulus test (Pack et al., 2002). I have so far not been able to trace comparable experiments in any other carnivoran.
More elaborate tests of visual cognition involve the ability to, for example, identify arbitrary objects as the same or different. The only demonstration of this ability in dogs that I know of used rather few stimuli, and it was found only in the auditory, not in the visual domain (Pietrzykowska & Soltysik, 1975ab), but it has been demonstrated more convincingly in pinnipeds, both in a common seal (Mauck & Dehnhardt, 2005) and in a sea lion (Hille et al., 2006); the seal even transferred the concept to a new stimulus dimension (Scholtyssek et al., 2013). Same/different discrimination seems to be spontaneous in chimpanzees, however (Oden et al., 1988), but is only acquired after extensive training with pigeons (Wright et al., 1988).
In the auditory modality, it is obvious from the large number of object names that one or two dogs have been trained to discriminate (Kaminski et al., 2004; Pilley & Reid, 2009) that dogs can discriminate human speech sounds; and some formal experimental work confirms this (Baru & Shmigidina, 1976; Ratcliffe and Reby, 2014). Evidence for discrimination of human speech sounds in the everyday life of other carnivorans is less obvious, but there are stronger formal demonstrations, for both cats (Hienz et al., 1996) and ferrets (Bizley et al., 2013). In chimpanzees, the various experiments on human language learning have demonstrated robust discrimination of substantial numbers of spoken words, on the order of 100 for both a chimpanzee and a bonobo (Brakke & Savage-Rumbaugh, 1995) even at a relatively early stage of the project. Horses and some other domestic animals must be able to discriminate at least a few human speech sounds, used as commands, but I have not yet found any quantitative estimates of their vocabulary.
Both dogs and cats have been shown to discriminate between the voices of different humans (e.g. Coutellier, 2006; Saito & Shinozuka, 2013), but I have not found any quantitative estimates of the number of humans who can be recognized, or the robustness of the discriminations. Recognition of individual conspecifics by voice appears to have been relatively neglected in dogs, though it has been demonstrated in some other carnivorans, including the Asian short-clawed otter (Lemasson et al., 2013), the dwarf mongoose (Sharpe et al., 2013) and pinnipeds (e.g. Van Parijs & Clark, 2006; Pitcher et al., 2010). It is highly developed in dolphins, through the use of "signature whistles" (Tyack, 1997), and also in some domestic animals: for example, in sheep it is used very early in life (Sèbe et al., 2010), and horses have been shown to link the voices of individual conspecifics with their visual appearance, demonstrating a cross-modal concept of the other individuals' identities (Proops et al., 2009).

Motor skills and sensorimotor co-ordination

Staying at the periphery of cognition, we can also consider the acquisition of motor skills and sensorimotor co-ordination. But here we have little basis for comparing dogs with other carnivorans. The whole sport of agility training with dogs bears witness to their capacity to learn new motor sequences, or adapt the ones they possess unconditionally, as do formal experiments such as those on dogs' ability to catch Frisbees (Shaffer et al., 2004). We lack comparable data from other carnivorans. However, in the past couple of decades, cat agility training has emerged as a sport (see, for example, Shaffer & Shaffer, undated), and more formal studies are likely to follow. Sea lions have also traditionally been trained for display purposes, in tasks involving close sensorimotor co-ordination such as balancing a ball, though again there is a lack of formal studies of their ability. Among the other social hunters we have considered, the ability of dolphins to learn, or even create (Pryor et al., 1969) novel motor sequences needs no underlining. Both chimpanzees, and many species of domestic animals, have also been trained for performance purposes. The most interesting case, however, is probably the horse; although the word "agility" is not used of horses, some equestrian sports such a show-jumping are quite similar to dog agility training, though the range of motor skills involved seems to be rather less than with dogs.

Physical cognition

By physical cognition, we refer to animals' (and humans') capacity to operate effectively on the world of objects – generally, objects smaller than, or comparable in size to, themselves. Research in this area has been strongly influenced by the importation into studies of animal cognition of ideas and procedures first devised for the investigation of human cognitive development, especially by Piaget and his collaborators (see Doré & Dumas, 1987). This has given us a number of more or less standard tasks that have been posed to a wide range of species. These tasks form the majority of what are often called "animal problem solving" situations, and the question being asked is usually not whether an animal can learn, or be trained, to solve a particular problem, but whether it does so spontaneously – that is to say, whether its ordinary cognitive capacities, as refined by everyday experience under normal rearing conditions, give it the ability to "see" a solution immediately. This description reminds us of the other important root of studies into animal physical cognition, Köhler's (1925) extended study of "insight" in chimpanzees (which in fact included a few experiments on other species, including dogs).

The general consensus of the literature is that dogs do poorly – unexpectedly poorly, in some authors' eyes – at physical cognition problems. Whether it is recognizing that a connecting tube will guide an object out of the line of fall dictated by gravity (Osthaus et al., 2003), string-pulling (e.g. Shepherd, 1915; Fischel, 1933; Osthaus et al., 2006; Range et al., 2012) and other support tasks (Müller et al., 2014), or opening a latch to escape from a box (Protopopov, see Windholz 1999), either all dogs have been found to fail to solve the problem spontaneously, or only a minority have succeeded. A particular case of physical cognition is the use of tools, and I have not found a convincing case of tool use in a dog; the nearest is a claim by Smith et al. (2013) that a captive dingo spontaneously moved a table around its enclosure in order to obtain out-of-reach food, echoing one of the tasks Köhler used with his chimpanzees.

Of course, there are exceptions, and also dissenting voices. Some of these tasks can be learned, even if they are not solved immediately, for example the support problem using planks (Müller et al., 2014). Dogs do solve the simplest string pulling tasks, with strings leading directly to the target object; where they fail is with multiple strings placed obliquely, or crossing each other; and a string-pulling experiment with vertically hanging ropes gave more positive results than the usual horizontal string situation (Hiestand, 2011) – though wolves in the same situation did better than dogs. Dogs have done relatively well at spontaneously solving sliding door (Bräuer et al., 2013), and container opening (Duranton et al., 2015; Horn et al., 2013) problems, and they have been shown to use the "solidity principle" to predict where a moving object will come to rest (Kundey et al., 2010). Furthermore, tasks involving the location and nature of hidden objects are generally solved well (e.g. Bräuer & Call, 2011), though not necessarily with any understanding of a hidden object's trajectory (e.g. Collier-Baker et al., 2004).

There are some indications that pet dogs' poor performance in object manipulation tasks may reflect their high degree of social skill in interacting with humans, so that rather than persisting at interacting with the task, they look to their owner (literally as well as metaphorically) for help in solving it. This has been seen as explaining why wolves (Frank & Frank, 1985), highly trained dogs (Marshall-Pescini et al., 2008), dogs with a working rather than a companion relationship with their owners (Topál et al., 1997) and dogs with a high level of inhibitory control (Müller et al., 2016) are sometimes found to outperform ordinary pet dogs in such tasks; while dogs raised in a restricted environment do worse (e.g. Clarke et al., 1951).

As regards our comparison groups, there is evidence that at least some other carnivorans do better than dogs at physical cognition tasks. Tested under comparable conditions, cats are no better than dogs at string-pulling problems (Whitt et al., 2009), but raccoons seem to solve them easily (Michels et al., 1961), and skunks (which are omnivorous carnivorans)

have been reported to do well at an analogous task (Johnson-Ulrich et al., 2015). Spotted hyenas appear to be skilled at physical problems (e.g. Benson-Amram & Holekamp, 2012), as do meerkats (Thornton & Samson, 2012); however Thornton and Samson are skeptical about the contribution of cognitive ability, rather than sheer persistence, to the solution of the problems they set their subjects. In their comprehensive review of tool use in animals, Bentley-Condit and Smith (2010) list a few reports of carnivorans showing what they consider to be true tool use, including giant pandas, a lion, American badgers, and two species of bear, in addition to the well-known use of sea otters using stones to open clam shells (Hall & Schaller, 1964); and Lindsey et al. (2004) report that African wild dogs (a species on which we have almost no cognitive data) learn to use fences to help them trap larger prey than they could otherwise kill.

The social hunters, however, include some species with apparently more advanced physical cognition than dogs. As well as hyenas, mentioned above, raptors have also been found to solve some physical problems, e.g. string pulling (a Harris hawk: Colbert-White et al., 2013) and box-opening (Chimango caracaras: Biondi et al., 2008). And despite their inability to manipulate anything with their limbs, bottlenose dolphins have been found to use tools (Krutzen et al., 2005). Chimpanzees are famously manipulative; and although Köhler (1925) found that they did not do well at complex string-pulling tasks, their spontaneous tool use in the wild has been thoroughly documented and studied since it was first reported by Goodall (1964).

Physical cognition has not been extensively studied in domestic animals other than cats, at least formally, and some reports of problem-solving by farm animals demonstrate little if anything more than basic operant conditioning. Gieling et al. (2011) list nothing that would fall within the field of physical cognition, as we are considering it here, in their comprehensive review of cognition in pigs, and the situation seems no different for most other domestic species. The exceptions are falcons, mentioned above, and pigeons: although most cognitive work with pigeons has been in the visual domain, there are a few studies of classic problem solving tasks, such as obstacle removal (Nakajima & Sato, 1993) and using a box to reach an inaccessible object (Epstein et al., 1984; Cook & Fowler, 2014). The consensus, however, is that pigeons' performance in such tasks can be accounted for by straightforward operant conditioning processes, and does not involve insight into the structure of the problem.

Spatial cognition

In considering spatial cognition, we need to distinguish small scale and large scale situations. The small scale involves an animal finding its way around within a small area, often its own home, a room in a laboratory, or at most a field – an area that the animal either knows well or can come to know well. The large scale involves navigation on the scale of kilometers, or even thousands of kilometers. It is not clear that the same cognitive capacities are required for both. It is not a hard and fast distinction: many animals will have both a core area (definitely small scale) and a much larger home range within which techniques normally used for large scale navigation might be appropriate. A guide dog leading its owner around a neighborhood or town, for example, is operating at this intermediate scale.

Dogs are certainly able to learn the characteristics of a small area well, as is shown by their performance in disappearing objects tests (Fiset et al, 2000), radial mazes (e.g. Macpherson & Roberts, 2010) and analogue tasks (Fabrigoule, 1974), or simple mazes (e.g. Fabrigoule, 1976). They use spatial cues preferentially over visual patterns (Dumas, 1998), though they do use landmarks to establish routes (e.g. Milgram et al., 1999; Fiset, 2009). Although Macpherson and Roberts found that their working memory for locations was quite low capacity, their longer term memory for places can be excellent. For example, they can find their way to a designated place by a novel route (e.g. Chapuis, 1975; Fabrigoule & Sagave, 1992), even when blindfolded (Cattet & Etienne, 2004), though not without error (Seguinot et al., 1998).

On the small scale, a significant problem in dogs' spatial behavior is their frequent inability to detour, especially at close range. Their problems with the more complex string pulling problems, and some other physical cognition tasks, can be traced to proximity error – the capture of attention, and behavior, by a nearby reward which actually has to be obtained by moving away from it, or at any rate not directly towards it (Osthaus et al., 2003, 2006). They can learn to avoid the proximity error by relying more on external cues (e.g. Fiset et al., 2007), but they still tend to perseverate on a past solution of this kind (Osthaus et al., 2010). Reports of large scale navigation by dogs, though not uncommon in the lay media, are largely anecdotal, and not to offer much more than can be found in Romanes (1886). It has recently been claimed that dogs show systematic orientation when defecating, and that this is mediated by a magnetic sense (Hart et al., 2013), but there is no direct evidence of the use of such a sense in navigation. In the wild, wolves can have very large home ranges (on the order of 10Km diameter: Benson & Patterson, 2015), and finding their way around these must require mechanisms that would allow long distance navigation.

Spatial cognition has not been studied in such detail in any other carnivorans, though several groups, particularly pinnipeds, range very widely or migrate seasonally, or both, so they must be capable of accurate long-distance navigation. Spotted hyenas have territories that can reach up to 320 Km^2, varying in size with the seasons (Trinkel et al., 2004). On the smaller scale, cats are good at locating hidden objects, though relying primarily on egocentric cues (Fiset and Doré, 1996); European badgers have been shown to learn simple spatial discriminations well, using landmarks (Mellgren & Roper, 1986); while American black bears were shown to have relatively modest spatial learning ability (Zamisch & Vonk, 2012). Some, but not all, carnivorans show sex differences in spatial ability (Perdue et al., 2011).

Among the other social hunters, dolphins like pinnipeds range widely (and some other odontocetes migrate seasonally), so they must have advanced navigational abilities. The most systematic tests of spatial ability at the medium scale, however, are in chimpanzees, which have been shown to have accurate knowledge and memory of the location of potential food sources within their (substantial) home ranges (Janmaat et al., 2013), and similar abilities were shown in captive tests (Mendes & Call, 2014) – though so far as is yet known this ability is called upon in their frugivorous rather than their carnivorous feeding behavior.

Basic spatial learning has been investigated in most domestic animals, for example in radial maze tests with pigs (Laughlin & Mendl, 2004), or finding food in a designated place in cows (Laca, 1998) and horses (McLean, 2004). The most detailed findings are with sheep, with many studies showing that they are highly sensitive to the distribution of different foods across a pasture, and remember it well (e.g. Edwards et al., 1996; Dumont & Petit, 1998; Hewitson et al., 2005). In terms of long range navigation, however, the abilities of the homing pigeon exceed those of any other domestic species; the literature is too extensive to be reviewed here, and too well known to need review. The point that does need to be made, however, is that these abilities were presumably developed in domestication, since although the ancestral rock dove may range over several kilometers for foraging purposes (Baldaccini et al., 2000), it does not use long distance navigation.

Social cognition

Because social cognition has been the focus of much of the recent research on dogs and wolves, it could easily have filled an entire paper on its own; however for the same reason, the results are relatively familiar, and I am taking this as an excuse to deal with them relatively briefly.

The simplest of all kinds of social cognition is using the presence, nature or behavior of another animal, whether conspecific or allospecific, as a cue in a learned task or in solving a problem. This has been the focus of an enormous amount of recent research in dogs, particularly in relation to dogs' use of points or gaze from humans. One major reason for this research focus is that dogs do seem to be highly sensitive to such signals. A second

major reason has been the "domestication hypothesis": the suggestion that domestication has selected for particular sensitivity to human cues in dogs (Hare & Tomasello, 2005). In consequence there has been considerable effort to use pointing or gaze tasks to compare dogs with wolves, or, in order to test alternative, ontogenetic, explanations of dogs' social skill, to compare groups of dogs whose life has involved different kinds or degrees of interaction with humans.

I do not need to pass all this literature in review. In summary, we can say that since the original formal demonstration of dogs' use of human points and gaze by Miklósi et al (1998), the phenomenon has been thoroughly explored and its limitations more or less determined. It seems likely that point and gaze use emerge very early in dog development (Riedel et el., 2008; Gácsi et al., 2009; Zaine et al., 2015), are somewhat different in dogs, or wolves, that have had less interaction with humans (Virányi et al., 2008; Udell et al., 2010), and in wolves rather than dogs – though the exact nature of the differences remains controversial (Miklósi et al., 2003; Udell et al., 2008).

There is less evidence of what might be thought of as the complementary phenomenon, dogs themselves using anything like a point. However, this obviously is a skill that has been selected for in particular dog breeds such as the pointers. Miklósi et al. (2000) have argued that in an experimental situation dogs used gaze alternation to draw their owners' attention to the location of a hidden toy.

Beyond using another animal as a cue, the next form of social cognition to be considered is the use of another animal as an aid to learning a task – what is generally referred to as social learning, where an observer animal learns a new task more quickly as a result of witnessing a demonstrator perform it. Within this field, it is standard practice to distinguish local or stimulus enhancement (the observer is attracted to an appropriate place or object), emulation (a term that has been used in different ways, but most often meaning that the observer's relevant motivation is raised), and motor imitation (the observer becomes more likely to make a particular response). All have been documented in dogs (local enhancement: Mersmann et al., 2011; emulation: Miller et al., 2009; imitation: Range et al., 2007). An interesting extension of social learning is the acquisition of what might be called an "imitation set", but is more often known as the "Do as I do" paradigm: the animal is trained to imitate arbitrary actions by the demonstrator on a specific signal. This has been successfully established in dogs (Topál et al., 2006), and even extended to get dogs to repeat remembered actions of the demonstrator (Fugazza et al., 2016).

More elaborate forms of social cognition are generally tied in, in one way or another, to the concept of theory of mind (Premack & Woodruff, 1978). Can an animal understand what another animal can perceive, and predict what it will understand? And if so, can it use that information for the purposes of deception, or to enter into the same state of mind (empathy)? Dogs react appropriately to what a human can or cannot know about a situation (Kaminski et al., 2009; Maginnity & Grace, 2014), a capacity referred to as "perspective taking" and seen as evidence for theory of mind, and though this ability is not seen in all dogs, it can be seen in wolves (Udell et al., 2011). Dogs also respond differently to humans who habitually deceive them about the location of food, compared with truthful humans (Petter et al., 2009; Takaoka et al., 2015), though the only suggestion I have found that dogs themselves engage in deception is in connection with play (Mitchell & Thompson, 1993).

The question of whether dogs display empathy has largely been investigated in relation to humans, rather than to conspecifics, and the answer is moot. There have been a series of investigations of contagious yawning, a behavior often taken to indicate empathy, and it is clear that dogs do show this phenomenon. While the interpretation of the data is still controversial, at least the latest studies (Silva et al., 2012; Romero et al., 2013) strongly suggest the involvement of social motivation. Romero et al. (2014) have now shown that these results extend to wolves. More generally, Custance and Mayer (2012) showed that dogs tend to show submissive (and therefore perhaps comforting) behavior towards people showing visible distress, though they argued that that could be due to mere emotional

contagion. A further approach to empathy is the idea that dogs would seek help for a person in distress or danger is controversial: Macpherson and Roberts (2006) argued that they would not, while Bräuer et al. (2013) claim that they will do so under at least some circumstances.

Both perspective-taking and empathy should, in principle, help animals solve problems that require co-operation. Two recent studies have reported some degree of co-operation in problem-solving by dogs, in a door-sliding task (Bräuer et al., 2013), the standard two-rope task (Ostojić & Clayton, 2014), and Range and Virányi (2015) have argued that co-cooperativeness is in fact an inherent quality of wolves, and contributed greatly to their successful domestication as dogs.

Turning to comparisons, there is little formal evidence available about social cognition in other carnivorans. Benson-Amram et al. (2014) found only weak evidence for it in spotted hyenas' problem solving, with local or stimulus enhancement as the most likely explanation. When it comes to non-carnivoran social hunters, however, there is copious evidence of imitation in both chimpanzees and bottlenose dolphins, and in these species it does seem to be a specifically social skill. For example, chimpanzees can acquire tool use by observation of others, and this seems to depend on witnessing an animate other using the tool (Hopper et al., 2015). Furthermore, "Do as I do" responding can be established: Hayes and Hayes (1952) used it in their attempt to teach the chimpanzee Vicki human speech, and while they did not succeed in getting her to copy speech sounds (probably because of anatomical limitations), she readily imitated physical skills. In a review of the literature on dolphin imitation, Herman (2002) concluded that they have a generalized and highly flexible capacity for imitative acts. Other domestic animals show no such enhanced tendency to social learning: for example, in a detour task, horses did not profit from seeing a conspecific take the detour (Rorvang et al., 2015). Pigs are at least able to use the behavior of others to help them find food more quickly (Held et al., 2000), and they show some signs of perspective taking (Held et al., 2001), though the authors of that study are cautious as to whether their results imply theory of mind.

I have found no discussion of deception in carnivorans other than dogs, but there is much discussion of whether it is shown by chimpanzees. Despite early claims (Woodruff & Premack, 1979), the experimental evidence for deception by chimpanzees is weak; however they do seem to conceal food from potential rivals (Hare et al., 2006; Osvath & Karvonen, 2012), behavior which also reflects future planning, discussed further below. The deceptive use of social signals, which has been the subject of much discussion in primates in general, has been reported for chimpanzees in natural situations, e.g. Slocombe & Zuberbühler (2007). But there is no evidence of deception in any of the other social hunters we have considered, or in non-carnivoran domestic species.

Similarly, I have found no claims for empathy in carnivorans other than dogs and wolves, but there is copious and longstanding evidence for it in chimpanzees, both from formal experimental tasks (e.g. Povinelli et al., 1992) and in more natural social situations (reviewed by O'Connell, 1995); it has not, apparently, been studied in dolphins – the simplest paradigm, contagious yawning, would be hard to apply in an aquatic species. Spontaneous helping behavior has also been reported in chimpanzees (Greenberg et al., 2010); it is widely claimed anecdotally in dolphins, but formal demonstrations are lacking. Co-operation has been demonstrated in spotted hyena problem solving (Drea & Carter, 2009), but I know of no other formal demonstrations in carnivorans other than dogs. It has been extensively studied in chimpanzees, and is clearly something they are capable of, though only if the social conditions are right (e.g. Melis et al., 2006). Dolphins similarly often appear to be co-operating in natural situations, but formal experiments do not always find successful co-operation: a recent report using an analogue of the two-rope task, however, is more convincing (Kuczaj et al., 2015). Once again, I have found no formal studies of co-operation in domestic animals other than dogs.

Self-consciousness and mental time travel

Linked to the question of theory of mind is the possibility of self-consciousness. The standard way of examining this in animals is the mirror-mark test, pioneered by Gallup (1970) for use with chimpanzees. I know of no evidence that dogs respond to their image in a mirror, following marking, in the same way as chimpanzees (and humans), though Gatti (2016) has claimed that an alternative way of approaching the problem, through dogs' own urine marking, gives comparable evidence of self-awareness.

A different way of approaching the question of an animal's awareness of self is through the possibility of what Suddendorf and Corballis (1997) call "mental time travel" – the ability to project oneself into past events, through episodic memory, or future events, through episodic future thought, or planning. Tulving (1972), who introduced the term episodic memory, subsequently argued that these abilities require "autonoetic consciousness", i.e. knowledge of the self (Tulving, 1985). Although many authors have claimed to show an analogue of human episodic memory in other animals (the "what-where-when" test introduced by Clayton & Dickinson, 1998), comparable studies with dogs have only shown an association of "what" and "where" that does not qualify as a full analogue (Kaminski et al., 2008; Fujita et al., 2012).

The comparisons in this area can be dealt with summarily. The mirror-mark test was first developed for chimpanzees, and although it does not work with every individual, and there has been controversy over its interpretation, the basic result seems to be well established (Heyes, 1994; Gallup et al., 1995). And despite the difficulties of carrying out parallel studies with an animal that cannot use its limbs to touch most parts of its body, there are several demonstrations that dolphins, too, respond by inspection to a mark placed on their body (Marten & Psarakos, 1995; Reiss & Marino, 2001). There are no comparable reports for other carnivorans, nor for non-carnivoran domestic species. Apart from a field study of apparently planful caching in a South American mustelid, the tayra (Soley & Alvarado-Diaz), there are no formal studies of episodic memory or planning in carnivorans other than dogs and wolves, nor in non-carnivoran domestic species. Surprisingly, I have so far found no direct studies of episodic memory in chimpanzees or dolphins, but there has been a spate of investigations of the other type of mental time travel, planning and intention, in chimpanzees. For example chimpanzees produce tools for future use in the laboratory (Bräuer & Call, 2015), direct their travels with apparent forethought within a computerized maze (Beran et al., 2015) or in their home range in the wild (Ban et al., 2014; Janmaat et al., 2014). Again the interpretation of these results remains controversial (Osvath & Osvath, 2008; Suddendorf et al., 2009), but there seems little doubt that chimpanzees show a kind of future-oriented behavior that has not been demonstrated in dogs or, indeed, in our other comparison species.

The comparative intelligence of dogs

As I have reviewed the different areas of cognition, I have deliberately not made judgements on the relative abilities of dogs. The time has come, however, to do so. The following conclusions seem to be in order.

- Except for some (sometimes contested) details of the way dogs use the behavior of humans as cues, we have found no evidence of substantial differences in cognition between dogs in general and wolves, though particular breeds of dogs, or dogs reared under particular circumstances may show inferior performance.
- We have unfortunately little data on cognition in any of the canids closely related to dogs, or on the other clearly identifiable social hunters among the carnivorans (the African wild dog and the spotted hyena), to draw strong generalizations about their performance relative to dogs. However from what we do know – mainly about spotted hyenas – there is no reason to think that their performance is worse than that of dogs, and in some cases it seems to be better.
- Looking at the carnivorans more widely, dogs have clearly been trained in more tasks,

and sometimes more successfully, than any other. This makes comparisons difficult. It would be particularly useful to have more data on cat cognition, because cats share a long history of domestication with dogs, and also like dogs are often kept as companions or aesthetic objects rather than for use or food; but the days are long gone when we could make a point for point comparison of dog and cat cognition, with roughly equal amounts of data on each, as Doré and Goulet (1992) did. However, there are clearly some tasks, particularly in the area of physical cognition including tool use, where even the scant data we have suggest that there are other carnivorans who succeed better than dogs. There are also specialized natural tasks, such as long-range navigation and scatter hoarding, for which some other carnivorans are cognitively equipped while, so far as we yet know, dogs are not.

- Considering the non-carnivorous social hunters draws in two taxonomic groups, the chimpanzees and bonobos and the bottlenose dolphins, whose cognitive capacities are clearly superior to those of dogs on quite a range of tests, including many in the area of social cognition where dogs tend to excel over other carnivorans
- Although there is a growing literature on domestic animal cognition, it contains few reports of capacities superior to those shown by dogs. The detailed work that has been done on face recognition in sheep, and the wider literature on pattern recognition in pigeons, may well demonstrate superior capacities to those of dogs, but we do not yet have as detailed an account of visual cognition in dogs to compare it with. The one outstanding example is in navigation, where pigeons' homing capacities (presumably developed in the domestic context) far exceed anything that we have experimental evidence for in dogs. It is unfortunate that we have relatively little formal knowledge so far of cognition in domestic equids or tamed raptors, because these are two groups that, like dogs, have been kept to work co-operatively with humans, so that similar social cognition might have developed. In both cases there is of course a great deal of practitioner knowledge, and as this becomes integrated with scientific study, this line of comparison should become more fruitful.
- The discussion so far exposes what might seem a weakness in the comparative method adopted in this paper. I have been comparing dogs with other carnivorans, other social hunters, and other domestic animals. The implication is that the answer to Coppinger and Coppinger's (2016) question, "What is a dog?" is precisely that it is an animal that belongs to all three of those groups; and all three of those qualities contribute to the unique cognitive position of dogs. On this basis, one might argue that one should compare social hunters with solitary hunters or herbivores, and domestic with wild species, in other taxa, to see whether those two factors add to the phylogenetic variations in cognition that seem obvious when we compare dogs with apes in general, or cetaceans in general (for example). If a gorilla or an orangutan's cognition excels that of a dog in just the same way as a chimpanzee's does, it would seem that phylogenetic factors trump ecological ones in determining cognitive capacity.

There is, indeed, no doubt that a fuller analysis like that does need to be done. However, I think that we can see, from the limited analysis so far, the direction in which it is likely to lead. Dog cognition looks quite a lot like that of other carnivorans, especially other closely related carnivorans; but it also looks somewhat like that of unrelated social hunters. The evidence that it has anything in common with that of other domestic animals in general is weak so far, but the most interesting comparators have not yet been fully investigated.

The analysis so far also makes another point clear. There is no current case for canine exceptionalism: we have not yet found evidence that dog cognition is very different from what we would expect of a domesticated socially hunting carnivoran.

The contribution of studies on dogs to our knowledge of comparative cognition

So, finally, what have the extensive studies of dog cognition of the past two decades brought to comparative cognition in general? I want to argue that there have been several major contributions. Dog cognition may not be exceptional, but dogs are certainly exceptional cognitive research subjects. There have some often rehearsed practical advantages: dogs are available in much larger numbers than any interesting comparator species except cats and horses; they do not have to be studied in captivity, or kept in laboratories, so the costs of studying them are much lower than for most of the other species we have mentioned; and they have been trained, over the millennia, in a range of cognitively interesting tasks.
These are essentially methodological points, but there are more substantive contributions as well. Our knowledge of non-humans' understanding of pointing, gaze, and other human signals has been greatly expanded through studies on dogs. The same literature has led to much more informed theorizing about the domestication process, so that earlier hypotheses about it now look frankly speculative. There are several fields of cognition – empathy, for example – where almost our only non-primate evidence comes from dogs, and the number of these seems likely to grow because the cooperativeness of dogs means that more complex research designs can be carried through than could be contemplated with less obliging subjects. And although dogs may not be typical carnivores, or typical social hunters, or typical domestic animals, what we know about cognition in all those groups consists to a substantial extent of what we know about dog cognition.
A comparative approach seems like the antithesis of the "model organism" approach to biology. The comparative approach recognizes that there is no such thing as a generalized animal, only particular animals – that, indeed, is the reason I gave at the beginning of this paper for comparing dogs with a principled selection of species, rather than other animals in general. Nonetheless, it is clear that we cannot explore every species' cognition in detail, any more than we can compare dog cognition with that of every other species. We have to understand the cognition in a few species really well, and then we can use that understanding as a framework to design investigation of cognition of other species as they become of interest. The flowering of work on dog cognition this century has placed dogs squarely within the small set of species whose cognition we can claim to understand reasonably well. It is a highly valuable addition because as a carnivoran, a social hunter, and a domestic animal, it is unlike most of its other members. As someone whose interest is essentially in comparative cognition, I hope that we can now begin to use our knowledge of dog cognition to go beyond the study of dogs, and look at more of the comparator species. And, of course, in doing so, we will also expand our understanding of what, fundamentally, a dog uniquely is.

References

Attard, M.R.G., Chamoli, U., Ferrara, T.L., Rogers, T.L., Wroe, S., 2011. Skull mechanics and implications for feeding behaviour in a large marsupial carnivore guild: the thylacine, Tasmanian devil and spotted-tailed quoll. Journal of Zoology 285, 292-300.

Bailey, I., Myatt, J.P., Wilson, A.M., 2013. Group hunting within the Carnivora: physiological, cognitive and environmental influences on strategy and cooperation. Behavioral Ecology and Sociobiology 67, 1-17.

Baldaccini, N.E., Giunchi, D., Mongini, E., Ragionieri, L., 2000. Foraging flights of wild rock doves *(Columba l. livia*): a spatio-temporal analysis. Italian Journal of Zoology 67, 371-377.

Ban, S.D., Boesch, C., Janmaat, K.R.L., 2014. Tai chimpanzees anticipate revisiting high-valued fruit trees from further distances. Animal Cognition 17, 1353-1364.

Baru, A.V., Shmigidina, G.N., 1976. Role of auditory-cortex in discrimination of synthesized vowels by dogs. Zhurnal Vysshei Nervnoi Deyatelnosti Imeni I P Pavlova 26, 1165-1173.

Bednarz, J.C., 1988. Cooperative hunting in Harris' hawks (*Parabuteo unicinctus*). Science 239, 1525-1527.

Bekoff, M., 1977. Canis latrans. Mammalian Species 79, 1-9.

Bensky, M.K., Gosling, S.D., Sinn, D.L., 2013. The world from a dog's point of view: A review and synthesis of dog cognition research. Advances in the Study of Behavior 45, 209-406.

Benson-Amram, S., Holekamp, K.E., 2012. Innovative problem solving by wild spotted hyenas. Proceedings of the Royal Society B: Biological Sciences 279, 4087-4095.

Benson-Amram, S., Heinen, V.K., Gessner, A., Weldele, M.L., Holekamp, K.E., 2014. Limited social learning of a novel technical problem by spotted hyenas. Behavioural Processes 109, 111-120.

Benson, J.F., Patterson, B.R., 2015. Spatial overlap, proximity, and habitat use of individual wolves within the same packs. Wildlife Society Bulletin 39, 31-40.

Bentley-Condit, V.K., Smith, E.O., 2010. Animal tool use: current definitions and an updated comprehensive catalog. Behaviour 147, 185-221.

Beran, M.J., Parrish, A.E., Futch, S.E., Evans, T.A.,Perdue, B.M., 2015. Looking ahead? Computerized maze task performance by chimpanzees (*Pan troglodytes*), Rhesus Monkeys *(Macaca mulatta*), Capuchin Monkeys (*Cebus apella*), and Human Children (*Homo sapiens*). Journal of Comparative Psychology 129, 160-173.

Biondi, L.M., Bo, M.S., Vassallo, A.I., 2008. Experimental assessment of problem solving by Milvago chimango (Aves : Falconiformes). Journal of Ethology 26, 113-118.

Bizley, J.K., Walker, K.M.M., King, A.J., Schnupp, J.W.H., 2013. Spectral timbre perception in ferrets: Discrimination of artificial vowels under different listening conditions. Journal of the Acoustical Society of America 133, 365-376.

Blasco, R., Finlayson, C., Rosell, J., Marco, A.S., Finlayson, S., Finlayson, G., Negro, J.J., Pacheco, F.G., Vidal, J.R., 2014. The earliest pigeon fanciers. Scientific Reports 4, 5971.

Brakke, K.E., Savage-Rumbaugh, E.S., 1995. The development of language skills in bonobo and chimpanzee: I Comprehension. Language and Communication 15, 121-148.

Bräuer, J., Call, J., 2011. The magic cup: Great apes and domestic dogs (*Canis familiaris*) individuate objects according to their properties. Journal of Comparative Psychology 125, 353-361.

Bräuer, J., Bos, M., Call, J., Tomasello, M., 2013. Domestic dogs (*Canis familiaris*) coordinate their actions in a problem-solving task. Animal Cognition 16, 273-285.

Bräuer, J., Call, J., 2015. Apes produce tools for future use. American Journal of Primatology, 77 254-263.

Brush, F.R., Brush, E.S., Solomon, R.L., 1955. Traumatic avoidance learning: the effects of CS-US interval with a delayed-conditioning procedure. Journal of Comparative & Physiological Psychology 48, 285-293.

Cattet, J., Etienne, A.S., 2004. Blindfolded dogs relocate a target through path integration. Animal Behaviour 68, 203-212.

Cavoto, K.K., Cook, R.G., 2001. Cognitive precedence for local information in hierarchical stimulus processing by pigeons. Journal of Experimental Psychology: Animal Behavior Processes 27, 3-16.

Chapuis, N., 1975. Inverse pathway learning in the dog. Cahiers de Psychologie 18, 219-228.

Clarke, R.S., Heron, W., Fetherstonhaugh, M.L., Forgays, D.G., Hebb, D.O., 1951. Individual differences in dogs: Preliminary report on the effects of early experience. Canadian Journal of Psychology 5, 150-156.

Clayton, N.S., Dickinson, A., 1998. Episodic-like memory during cache recovery by scrub jays. Nature 395, 272-274.

Colbert-White, E.N., McCord, E.M., Sharpe, D.I., Fragaszy, D.M., 2013. String-pulling behaviour in a Harris's Hawk *Parabuteo unicinctus*. Ibis 155, 611-615.

Collier-Baker, E., Davis, J.M., Suddendorf, T., 2004. Do dogs (*Canis familiaris*) understand invisible displacement? Journal of Comparative Psychology 118, 421-433.

Cook, R.G., Fowler, C., 2014. "Insight" in pigeons: Absence of means-end processing in displacement tests. Animal Cognition 17, 207-220.

Coppinger, R., Coppinger, L., 2016. What is a dog? Chicago: University of Chicago Press.

Coutellier, L., 2006. Are dogs able to recognize their handler's voice? A preliminary study. Anthrozoös 19, 278-284.

Custance, D., Mayer, J., 2012. Empathic-like responding by domestic dogs (*Canis familiaris*) to distress in humans: an exploratory study. Animal Cognition 15, 851-859.

Doré, F.Y., Dumas, C., 1987. Psychology of animal cognition: Piagetian studies. Psychological Bulletin 102, 219-233.

Doré, F.Y., Goulet, S., 1992. Cognition in carnivorous mammals: Cats and dogs. Psychologie Française 37, 65-72.

Drea, C.M., Carter, A.N., 2009. Cooperative problem solving in a social carnivore. Animal Behaviour 78, 967-977.

Dumont, B., Petit, M., 1998. Spatial memory of sheep at pasture. Applied Animal Behaviour Science 60, 43-53.

Duranton, C., Rodel, H.G., Bedossa, T., Belkhir, S., 2015. Inverse sex effects on performance of domestic dogs (*Canis familiaris*) in a repeated problem-solving task. Journal of Comparative Psychology 129, 84-87.

Edwards, G.R., Newman, J.A., Parsons, A.J., Krebs, J.R., 1996. The use of spatial memory by grazing animals to locate food patches in spatially heterogeneous environments: an example with sheep. Applied Animal Behaviour Science 50, 147-160.

Epstein, R., Kirshnit, C.E., Lanza, R.P., Rubin, L.C., 1984. Insight in the pigeon: Antecedents and determinants of an intelligent performance. Nature 308, 61-62.

Fabrigoule, C., 1974. Experimentation on spatial learning in the dog: Learning of progressive exclusion. Cahiers de Psychologie 17, 91-110.

Fabrigoule, C., 1976. Cue selection with the dog in a double 'T' maze has multiple solutions. Annee Psychologique, 59-381.

Fagot, J., Tomonaga, M., 1999. Global and local processing in humans *(Homo sapiens*) and chimpanzees (*Pan troglodytes*): use of a visual search task with compound stimuli. Journal of Comparative Psychology 113, 3-12.

Fields, P.E., 1936. Studies in concept formation: III. A note on the retention of visual figure discriminations. Journal of Comparative Psychology 21, 131-136.

Figueirido, B., Janis, C.M., 2011. The predatory behaviour of the thylacine: Tasmanian tiger or marsupial wolf? Biology Letters 7, 937.

Fischel, W., 1933. The behavior of dogs with double goal setting and two possible actions/Das Verhalten von Hunden bei doppelter Zielsetzung und doppelter Handlungsmoeglichkeit. Zeitschrift fuer Vergleichende Physiologie 19, 170-182.

Fiset, S., Doré, F.Y., 1996. Spatial encoding in domestic cats (*Felis catus*). Journal of Experimental Psychology: Animal Behavior Processes 22, 420-437.

Fiset, S., Gagnon, S., Beaulieu, C., 2000. Spatial encoding of hidden objects in dogs (*Canis familiaris*). Journal of Comparative Psychology 114, 315-324.

Fiset, S., Beaulieu, C., LeBlanc, V., Dube, L., 2007. Spatial memory of domestic dogs (*Canis familiaris*) for hidden objects in a detour task. Journal of Experimental Psychology: Animal Behavior Processes 33, 497-508.

Fiset, S., 2009. Evidence for averaging of distance from landmarks in the domestic dog. Behavioural Processes 81, 429-438.

Frank, H., Frank, M.G., 1985. Comparative manipulation-test performance in ten-week-old wolves (*Canis lupus*) and Alaskan malamutes (*Canis familiaris*): A Piagetian interpretation. Journal of Comparative Psychology 99, 266-274.

Fugazza, C., Pogány, Á., Miklósi, Á., 2016. Do as I -- Did! Long-term memory of imitative actions in dogs (*Canis familiaris*). Animal Cognition 19, 263-269.

Fujita, K., Morisaki, A., Takaoka, A., Maeda, T., Hori, Y., 2012. Incidental memory in dogs (*Canis familiaris*): adaptive behavioral solution at an unexpected memory test. Animal Cognition 15, 1055-1063.

Gácsi, M., Kara, E., Belenyi, B., Topál, J., Miklósi, Á., 2009. The effect of development and individual differences in pointing comprehension of dogs. Animal Cognition 12, 471-479.

Gallagher, T., 2008. Falcon fever. Boston: Houghton Mifflin.

Gallup, G.G., Povinelli, D.J., Suarez, S.D., Anderson, J.R., Lethmate, J., Menzel, E.W., 1995. Further reflections on self-recognition in primates. Animal Behaviour 50, 1525-1532.

Gallup, G.G., 1970. Chimpanzees: Self-recognition. Science 167, 86-87.

Gatti, R.C., 2016. Self-consciousness: beyond the looking-glass and what dogs found there. Ethology Ecology & Evolution 28, 232-240.

Gazda, S.K., Connor, R.C., Edgar, R.K., Cox, F., 2005. A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. Proceedings of the Royal Society B: Biological Sciences 272, 135-140.

Gieling, E.T., Nordquist, R.E., van der Staay, F.J., 2011. Assessing learning and memory in pigs. Animal Cognition 14, 151-173.

Goodall, J., 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. Nature, 201, 1264-1266.

Green, P.A., Van Valkenburgh, B., Pang, B., Bird, D., Rowe, T., Curtis, A., 2012. Respiratory and olfactory turbinal size in canid and arctoid carnivorans. Journal of Anatomy 221, 609-621.

Greenberg, J.R., Hamann, K., Warneken, F., Tomasello, M., 2010. Chimpanzee helping in collaborative and noncollaborative contexts. Animal Behaviour 80, 873-880.

Hall, K.R.L., Schaller, G.B., 1974. Tool-using behavior of the California sea otter. Journal of Mammalogy 45, 287-298.

Hare, B., Tomasello, M., 2005. Human-like social skills in dogs? Trends in Cognitive Sciences 9, 439-444.

Hare, B., Call, J., Tomasello, M., 2006. Chimpanzees deceive a human competitor by hiding. Cognition 101, 495-514.

Hart, V., Novákova, P., Malkemper, E.P., Begall, S., Hanzal, V., Ježek, M., Kušta, T., Němcová, V., Adámková, J., Benediktová, K., Červený, J., Burda, H., 2013. Dogs are sensitive to small variations of the Earth's magnetic field. Frontiers in Zoology 10, 80.

Hayes, K. J., Hayes, C., 1952. Imitation in a home-raised chimpanzee. Journal of Comparative and Physiological Psychology 45, 450-459.

Hayward, M.W., 2006. Prey preferences of the spotted hyaena (*Crocuta crocuta*). Journal of Zoology 270, 606-614.

Hayward, M.W., O'Brien, J., Hofmeyr, M., Kerley, G.I.H., 2006. Prey preferences of the African wild dog *Lycaon pictus* (Canidae: Carnivora): Ecological requirements for conservation. Journal of Mammalogy 87, 1122-1131.

Hayward, M.W., Lyngdoh, S., Habib, B., 2014. Diet and prey preferences of dholes. (*Cuon alpinus*): dietary competition within Asia's apex predator guild. Journal of Zoology 294, 255-266.

Hector, D.P., 1986. Cooperative hunting and its relationship to foraging success and prey size in an avian predator. Ethology 73, 247-257.

Held, S., Mendl, M., Devereux, C., Byrne, R.W., 2000. Social tactics of pigs in a competitive foraging task: the 'informed forager' paradigm. Animal Behaviour 59, 569-576.

Held, S., Mendl, M., Devereux, C., Byrne, R.W., 2001. Behaviour of domestic pigs in a visual perspective taking task. Behaviour 138, 1337-1354.

Hepper, P.G., 1988. The discrimination of human odour by the dog. Perception 17, 549-554.

Herman, L.M., 2002. Vocal, social, and self-imitation by bottlenosed dolphins. In: Dautenhahn, K., Nehaniv, C.L., (Eds.), Imitation in animals and artifacts. Compex adaptive systems, 63-108. Cambridge, MA, US: MIT Press.

Hewitson, L., Dumont, B., Gordon, I.J., 2005. Response of foraging sheep to variability in the spatial distribution of resources. Animal Behaviour 69, 1069-1076.

Heyes, C.M., 1994. Reflections on self-recognition in primates. Animal Behaviour 47, 909-919.

Hienz, R.D., Aleszczyk, C.M., May, B.J., 1996. Vowel discrimination in cats: Acquisition effects of stimulus level, and performance in noise. Journal of the Acoustical Society of America 99, 3656-3668.

Hiestand, L., 2011. A comparison of problem-solving and spatial orientation in the wolf (*Canis lupus*) and dog (*Canis familiaris*). Behavior Genetics 41, 840-857.

Hille, P., Dehnhardt, G., Mauck, B., 2006. An analysis of visual oddity concept learning in a California sea lion (*Zalophus californianus*). Learning & Behavior 34, 144-153.

Hinde, R.A., Stevenson-Hinde, J., (Eds.), 1973. Constraints on learning. New York: Academic Press 148, 676-677.

Hobson, E.S., 1963. Feeding behavior in three species of sharks. Pacific Science 17, 171-194.

Hofreiter, M., Kreuz, E., Eriksson, J., Schubert, G., Hohmann, G., 2010. Vertebrate DNA in fecal samples from bonobos and gorillas: Evidence for meat consumption or artefact? PLOS One 5, e09419.

Holekamp, K.E., Sakai, S.T., Lundrigan, B.L., 2007. The spotted hyena *(Crocuta crocuta*) as a model system for study of the evolution of intelligence. Journal of Mammalogy 88, 545-554.

Hopkins, W.D., Washburn, D.A., 2002. Matching visual stimuli on the basis of global and local features by chimpanzees *(Pan troglodytes*) and rhesus monkeys *(Macaca mulatta*). Animal Cognition 5, 27-31.

Hopper, L.M., Lambeth, S.P., Schapiro, S.J., Whiten, A., 2015. The importance of witnessed agency in chimpanzee social learning of tool use. Behavioural Processes 112, 120-129.

Horn, L., Huber, L., Range, F., 2013. The importance of the secure base effect for domestic dogs: evidence from a manipulative problem-solving task. PLOS One 8, e65296.

Hyvarinen, H., Palviainen, A., Strandberg, U., Holopainen, I.J., 2009. Aquatic environment and differentiation of vibrissae: comparison of sinus hair systems of ringed seal, otter and pole cat. Brain Behavior and Evolution 74, 268-279.

Ihobe, H., 1992. Observations on the meat-eating behavior of wild bonobos *(Pan paniscus*) at Wamba, Republic of Zaire. Primates 33, 247-250.

Ihobe, H., 1997. Non-antagonistic relations between wild bonobos and two species of guenons. Primates 38, 351-357.

Janmaat, K.R.L., Ban, S.D., Boesch, C., 2013. Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. Animal Behaviour 86, 1183-1205.

Janmaat, K.R.L., Polansky, L., Ban, S.D., Boesch, C., 2014. Wild chimpanzees plan their breakfast time, type, and location. Proceedings of the National Academy of Sciences of the United States of America, 111, 16343–16348.

Jenkins, H.M., Barrera, F.J., Ireland, C., Woodside, B., 1978. Signal-centered action patterns of dogs in appetitive classical conditioning. Learning and Motivation 9, 272-296.

Johnson-Ulrich, Z., Vonk, J., Hoffmaster, E., 2015. Testing physical cognition in striped skunks with the slat-pulling task. Paper read at the meeting of the Comparative Cognition Society, April, Melbourne, FL.

Johnston, R.F., 1992. Evolution in the rock dove: skeletal morphology. Auk 109, 530-542.

Kalmus, H., 1955. The discrimination by the nose of the dog of individual human odours and in particular the odours of twins. British Journal of Animal Behaviour 3, 1-25.

Kaminski, J., Call, J., Fischer, J., 2004. Word learning in a domestic dog: Evidence for "fast mapping". Science 304, 1682-1683.

Kaminski, J., Fischer, J., Call, J., 2008. Prospective object search in dogs: mixed evidence for knowledge of What and Where. Animal Cognition 11, 367-371.

Kaminski, J., Bräuer, J., Call, J., Tomasello, M., 2009. Domestic dogs are sensitive to a human's perspective. Behaviour 146, 979-998.

Kendrick, K.M., Atkins, K., Hinton, M.R., Broad, K.D., Fabre-Nys, C., Keverne, B., 1995. Facial and vocal discrimination in sheep. Animal Behaviour 49, 1665-1676.

Kendrick, K.M., da Costa, A.P., Leigh, A.E., Hinton, M.R., Peirce, J.W., 2001. Sheep don't forget a face. Nature 414, 165-166.

Koehler, W., 1925. The mentality of apes. London: Routledge & Kegan Paul.

Krützen, M., Mann, J., Heithaus, M.R., Connor, R.C., Bejder, L., Sherwin, W.B., 2005. Cultural transmission of tool use in bottlenose dolphins. Proceedings of the National Academy of Sciences of the United States of America 102, 8939-8943.

Kuczaj, S.A., Winship, K.A., Eskelinen, H.C., 2015. Can bottlenose dolphins *(Tursiops truncatus*) cooperate when solving a novel task? Animal Cognition 18, 543-550.

Kundey, S.M.A., De Los Reyes, A., Taglang, C., Baruch, A., German, R., 2010. Domesticated dogs' (*Canis familiaris*) use of the solidity principle. Animal Cognition 13, 497-505.

Laca, E.A., 1998. Spatial memory and food searching mechanisms of cattle. Journal of Range Management 51, 370-378.

Laughlin, K., Mendl, M., 2004. Costs of acquiring and forgetting information affect spatial memory and its susceptibility to interference. Animal Behaviour 68, 97-103.

Lemasson, A., Mikus, M.A., Blois-Heulin, C., Lode, T., 2013. Social partner discrimination based on sounds and scents in Asian small-clawed otters (*Aonyx cinereus*). Naturwissenschaften 100, 275-279.

Lindsey, P.A., du Toit, J.T., Mills, M.G.L., 2004. Area and prey requirements of African wild dogs under varying habitat conditions: implications for reintroductions. South African Journal of Wildlife Research 34, 77-86.

Li, X., Li, W.H., Wang, H., Bayley, D.L., Cao, J., Reed, D.R., Bachmanov, A.A., Huang, L.Q., Legrand-Defretin, V., Beauchamp, G.K., Brand, J.G., 2006. Cats lack a sweet taste receptor. Journal of Nutrition 136, 1932S-1934S.

Li, X., Glaser, D., Li, W.H., Johnson, W.E., O'Brien, S.J., Beauchamp, G.K., Brand, J.G., 2009. Analyses of sweet receptor gene (*Tas1r2*) and preference for sweet stimuli in species of carnivora. Journal of Heredity 100, 90-100.

Mackintosh, N.J., 1974. The psychology of animal learning. London: Academic Press 67, 439-440.

Macpherson, K., Roberts, W.A., 2006. Do dogs (*Canis familiaris*) seek help in an emergency? Journal of Comparative Psychology 120, 113-119.

Macpherson, K., Roberts, W.A., 2010. Spatial memory in dogs (*Canis familiaris*) on a radial maze. Journal of Comparative Psychology 124, 47-56.

Maes, E., DeFilippo, G., Inkster, A.B., Lea, S.E.G., DeHouwer, J., D'Hooge, R., Beckers, T., Wills, A.J., 2015. Feature versus rule-based generalization in rats, pigeons and humans. Animal Cognition 18, 1267-1284.

Maginnity, M.E., Grace, R.C., 2014. Visual perspective taking by dogs (*Canis familiaris*) in a Guesser-Knower task: evidence for a canine theory of mind? Animal Cognition 17, 1375-1392.

Marshall-Pescini, S., Valsecchi, P., Petak, I., Accorsi, P.A., Previde, E.P., 2008. Does training make you smarter? The effects of training on dogs' performance (*Canis familiaris*) in a problem solving task. Behavioural Processes 78, 449-454.

Marten, K., Psarakos, S., 1995. Using self-view television to distinguish between self-examination and social behavior in the bottlenose dolphin *(Tursiops truncatus*). Consciousness and Cognition 4, 205-225.

Martin-Malivel, J., Okada, K., (2007). Human and chimpanzee face recognition in chimpanzees *(Pan troglodytes*): Role of exposure and impact on categorical perception. Behavioral Neuroscience 121, 1145-1155.

Mauck, B., Dehnhardt, G., 2005. Identity concept formation during visual multiple-choice matching in a harbor seal (*Phoca vitulina*). Learning & Behavior 33, 428-436.

Mayr, E., 1942. Systematics and the origin of species from the viewpoint of a zoologist. New York: Columbia University Press.

McAdam, D., 1964. Effects of positional relations between subject CS + US on shuttle-box

avoidance learning in cats. Journal of Comparative and Physiological Psychology, 58, 302-304.

McVey, J.M., Cobb, D.T., Powell, R.A., Stoskopf, M.K., Bobling, J.H., Waits, L.P., Moorman, C.E., 2013. Diets of sympatric red wolves and coyotes in northeastern North Carolina. Journal of Mammalogy 94, 1141-1148.

Melis, A.P., Hare, B., Tomasello, M., 2006. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. Animal Behaviour 72, 275-286.

Mellgren, R.L., Roper, T.J., 1986. Spatial learning and discrimination of food patches in the European badger (*Meles meles* L.). Animal Behaviour 34, 1129-1134.

Mendes, N., Call, J., 2014. Chimpanzees form long-term memories for food locations after limited exposure. American Journal of Primatology 76, 485-495.

Mersmann, D., Tomasello, M., Call, J., Kaminski, J., Taborsky, M., 2011. Simple mechanisms can explain social learning in domestic dogs (*Canis familiaris*). Ethology 117, 675-690.

Michels, K.M., Johnson, J.I., Pustek, J.J., 1961. Solution of patterned-strings problems by raccoons. Journal of Comparative and Physiological Psychology, 54, 439-441.

Miklósi, Á., Polgárdi, R., Topál, J., Csányi, V., 1998. Use of experimenter-given cues in dogs. Animal Cognition 1, 113-121.

Miklósi, Á., Polgárdi, R., Topál, J., Csányi, V., 2000. Intentional behaviour in dog-human communication: an experimental analysis of "showing" behaviour in the dog. Animal Cognition 3, 159-166.

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., Csányi, V., 2003. A simple reason for a big difference: Wolves do not look back at humans, but dogs do. Current Biology 13, 763-766.

Miklósi, Á., 2014. Dog cognition, behaviour and evolution, 2nd edn. Oxford: Oxford University Press.

Milgram, N.W., Adams, B., Callahan, H., Head, E., Mackay, B., Thirlwell, C., Cotman, C.W., 1999. Landmark discrimination learning in the dog. Learning & Memory 6, 54-61.

Miller, H.C., Rayburn-Reeves, R., Zentall, T.R., 2009. Imitation and emulation by dogs using a bidirectional control procedure. Behavioural Processes 80, 109-114.

Mitchell, R.W., Thompson, N.S., 1993. Familiarity and the rarity of deception: Two theories and their relevance to play between dogs (*Canis familiaris*) and humans (*Homo sapiens*). Journal of Comparative Psychology 107, 291-300.

Müller, C.A., Riemer, S., Viranyi, Z., Huber, L., Range, F., 2014. Dogs learn to solve the support problem based on perceptual cues. Animal Cognition 17, 1071-1080.

Müller, C.A., Riemer, S., Viranyi, Z., Huber, L., Range, F., 2016. Inhibitory control, but not prolonged object-related experience appears to affect physical problem-solving performance of pet dogs. PLOS One 11, e147753.

Nakajima, S., Sato, M., 1993. Removal of an obstacle: Problem-solving behavior in pigeons. Journal of the Experimental Analysis of Behavior 59, 131-145.

O'Connell, S.M., 1995. Empathy in chimpanzees: Evidence for theory of mind. Primates 36, 397-410.

Oden, D.L., Premack, D., Thompson, R.K.R., 1988. Spontaneous transfer of matching by infant chimpanzees *(Pan troglodytes*). Journal of Experimental Psychology: Animal Behavior Processes 14, 140-145.

Osthaus, B., Slater, A.M., Lea, S.E.G., 2003. Can dogs defy gravity? A comparison with the human infant and a non-human primate. Developmental Science 6, 489-497.

Osthaus, B., Lea, S.E.G., Slater, A.M., 2005. Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connections in a string-pulling task. Animal Cognition 8, 37-47.

Osthaus, B., Marlow, D., Ducat, P., 2010. Minding the gap: spatial perseveration error in dogs. Animal Cognition, *in press* as of June 2010.

Ostojić, L., Clayton, N.S., 2014. Behavioural coordination of dogs in a cooperative problem-

solving task with a conspecific and a human partner. Animal Cognition 17, 445-459.

Osvath, M., Osvath, H., 2008. Chimpanzee *(Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. Animal Cognition 11, 661-674.

Osvath, M., Karvonen, E., 2012. Spontaneous innovation for future deception in a male chimpanzee. PLOS One 7, e36782.

Pack, A.A., Herman, L.M., Hoffmann-Kuhnt, M., Branstetter, B.K., 2002. The object behind the echo: Dolphins *(Tursiops truncatus*) perceive object shape globally through echolocation. Behavioural Processes 58, 1-26.

Parr, L.A., Winslow, J.T., Hopkins, W.D., DeWaal, F.B.M., 2000. Recognizing facial cues: Individual discrimination by chimpanzees *(Pan troglodytes*) and rhesus monkeys *(Macaca mulatta*). Journal of Comparative Psychology 114, 47-60.

Pattison, K.F., Miller, H.C., Rayburn-Reeves, R., Zentall, T., 2010. The case of the disappearing bone: Dogs' understanding of the physical properties of objects. Behavioural Processes 85, 278-282.

Pavlov, I.P., 1927. Conditioned reflexes. London: Routledge and Kegan Paul.

Perdue, B.M., Snyder, R.J., Zhihe, Z., Marr, J., Maple, T.L., 2011. Sex differences in spatial ability: a test of the range size hypothesis in the order Carnivora. Biology Letters 7, 380-383.

Petter, M., Musolino, E., Roberts, W.A., Cole, M., 2009. Can dogs (*Canis familiaris*) detect human deception? Behavioural Processes 82, 109-118.

Pettit, M., 2010. The problem of raccoon intelligence in behaviourist America. British Journal For the History of Science 43, 391-421.

Pietrzykowska, B., Soltysik, S., 1975. A failure to train the "same-different" differentiation of photic stimuli in dogs. Acta Neurobiologiae Experimentalis 35, 27-38.

Pietrzykowska, B., Soltysik, S., 1975. Transfer of the "same-different" differentiation task in dogs. Acta Neurobiologiae Experimentalis 35, 39-50.

Pilley, J.W., Reid, A.K., 2009. Border collie demonstrates referential understanding of words. Conference on Comparative Cognition.

Pinc, L., Bartoş, L., Reslová, A., Kotrba, R., 2011. Dogs discriminate identical twins. PLOS One 6, e20704.

Pitcher, B.J., Harcourt, R.G., Charrier, I., 2010. The memory remains: long-term vocal recognition in Australian sea lions. Animal Cognition 13, 771-776.

Pitteri, E., Mongillo, P., Carnier, P., Marinelli, L., 2014. Hierarchical stimulus processing by dogs (*Canis familiaris*). Animal Cognition 17, 869-877.

Povinelli, D.J., Nelson, K.E., Boysen, S.T., 1992. Comprehension of role reversal in chimpanzees: evidence of empathy. Animal Behaviour 43, 633-640.

Premack, D., Woodruff, G., 1978. Does the chimpanzee have a theory of mind? Behavioral and Brain Sciences 1, 515-526.

Proops, L., McComb, K., Reby, D., 2009. Cross-modal individual recognition in domestic horses (*Equus caballus*). Proceedings of the National Academy of Sciences of the United States of America 106, 947-951.

Pryor, K.W., Haag, R., O'Reilly, J., 1969. The creative porpoise: Training for novel behavior. Journal of the Experimental Analysis of Behavior 12, 653-661.

Racca, A., Amadei, E., Ligout, S., Guo, K., Meints, K., Mills, D., 2010. Discrimination of human and dog faces and inversion responses in domestic dogs (*Canis familiaris*). Animal Cognition 13, 525-533.

Range, F., Moslinger, H., Virányi, Z., 2012. Domestication has not affected the understanding of means-end connections in dogs. Animal Cognition 15, 597-607.

Range, F., Virányi, Z., 2015. Tracking the evolutionary origins of dog-human cooperation: the "Canine Cooperation Hypothesis". Frontiers in Psychology, 5, 1582.

Range, F., Virányi, Z., Huber, L., 2007. Selective imitation in domestic dogs. Current Biology

17, 1-5.

Ratcliffe, V.F., Reby, D., 2014. Orienting asymmetries in dogs' responses to different communicatory components of human speech. Current Biology 24, 2908-2912.

Reiss, D., Marino, L., 2001. Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. Proceedings of the National Academy of Sciences of the United States of America 98, 5937-5942.

Riedel, J., Schumann, K., Kaminski, J., Call, J., Tomasello, M., 2008. The early ontogeny of human-dog communication. Animal Behaviour 75, 1003-1014.

Robbins, W.D., Renaud, P., 2016. Foraging mode of the grey reef shark, *Carcharhinus amblyrhynchos*, under two different scenarios. Coral Reefs 35, 253-260.

Romanes, G.J., 1886. Animal intelligenc (4th ed). London: Kegan Paul, Trench.

Romero, T., Konno, A., Hasegawa, T., 2013. Familiarity bias and physiological responses in contagious yawning by dogs support link to empathy. PLOS One 8, e71365.

Romero, T., Ito, M., Saito, A., Hasegawa, T., 2014. Social modulation of contagious yawning in wolves. PLOS One 9, e105963.

Sato, A., Kanazawa, S., Fujita, K., 1997. Perception of object unity in a chimpanzee *(Pan troglodytes*). Japanese Psychological Research 39, 191-199.

Saito, A., Shinozuka, K., 2013. Vocal recognition of owners by domestic cats *(Felis catus*). Animal Cognition 16, 685-690.

Scholtyssek, C., Kelber, A., Hanke, F.D., Dehnhardt, G., 2013. A harbor seal can transfer the same/different concept to new stimulus dimensions. Animal Cognition 16, 915-925.

Sèbe, F., Duboscq, J., Aubin, T., Ligout, S., Poindron, P., 2010. Early vocal recognition of mother by lambs: contribution of low- and high-frequency vocalizations. Animal Behaviour 79, 1055-1066.

Seguinot, V., Cattet, J., Benhamou, S., 1998. Path integration in dogs. Animal Behaviour 55, 787-797.

Sekuler, A.B., Lee, J.A.J., Shettleworth, S.J., 1996. Pigeons do not complete partly occluded figures. Perception 25, 1109-1120.

Seligman, M.E.P., 1970. On the generality of the laws of learning. Psychological Review 77, 406-418.

Seward, J.P., Humphrey, G.L., 1967. Avoidance learning as a function of pretraining in cat. Journal of Comparative and Physiological Psychology, 63, 338-341.

Shaffer, D.M., Krauchunas, S.M., Eddy, M., McBeath, M.K., 2004. How dogs navigate to catch Frisbees. Psychological Science, 15, 437-441.

Shaffer, C., Shaffer, L., (undated). Agility training for your cat. http://agility.cfa.org/clicker-training.shtml, downloaded 31st March 2016.

Sharpe, L.L., Hill, A., Cherry, M.I., 2013. Individual recognition in a wild cooperative mammal using contact calls. Animal Behaviour 86, 893-900.

Shepherd, W.T., 1915. Tests on adaptive intelligence in dogs and cats, as compared with adaptive intelligence in Rhesus monkeys. American Journal of Psychology 26, 211-216.

Shettleworth, S.J., 2010. Cognition, evolution and behavior, 2nd edn. Oxford: Oxford University Press.

Silva, K., Bessa, J., de Sousa, L., 2012. Auditory contagious yawning in domestic dogs (*Canis familiaris*): first evidence for social modulation. Animal Cognition 15, 721-724.

Slocombe, K.E., Zuberbühler, K., 2007. Chimpanzees modify recruitment screams as a function of audience composition. Proceedings of the National Academy of Sciences of the United States of America 104, 17228-17233.

Smith, B.P., Appleby, R.G., Litchfield, C.A., 2012. Spontaneous tool-use: An observation of a dingo (*Canis dingo*) using a table to access an out-of-reach food reward. Behavioural Processes 89, 219-224.

Solomon, R.L., Wynne, L.C., 1953. Traumatic avoidance learning: acquisition in normal dogs.

Psychological Monographs 67, 19.

Somppi, S., Tornqvist, H., Kujala, M.V., Hanninen, L., Krause, C.M., Vainio, O., 2016. Dogs evaluate threatening facial expressions by their biological validity: evidence from gazing patterns. PLOS One 11, e143047.

Stander, P.E., 1992. Cooperative hunting in lions: The role of the individual. Behavioral Ecology and Sociobiology 29, 445-454.

Stanford, C.B., Wallis, J., Matama, H., Goodall, J., 1994. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982-1991. American Journal of Physical Anthropology 94, 213-228.

Suddendorf, T., Corballis, M.C., 1997. Mental time travel and the evolution of the human mind. Genetic Social and General Psychology Monographs 123, 133-167.

Suddendorf, T., Corballis, M.C., Collier-Baker, E., 2009. How great is great ape foresight? Animal Cognition 12, 751-754.

Surbeck, M., Fowler, A., Deimel, C., Hohmann, G., 2009. Evidence for the consumption of arboreal, diurnal primates by bonobos *(Pan paniscus*). American Journal of Primatology 71, 171-174.

Szetei, V., Miklósi, Á., Topál, J., Csányi, V., 2003. When dogs seem to lose their nose: an investigation on the use of visual and olfactory cues in communicative context between dog and owner. Applied Animal Behaviour Science 83, 141-152.

Takaoka, A., Maeda, T., Hori, Y., Fujita, K., 2015. Do dogs follow behavioral cues from an unreliable human? Animal Cognition 18, 475-483.

Teleki, G., 1973. The predatory behavior of wild chimpanzees. Lewisburg PA: Bucknell University Press.

Thorndike, E.L., 1898. Animal intelligence: An experimental study of the associative processes in animals. New York: Macmillan.

Thornton, A., Samson, J., 2012. Innovative problem solving in wild meerkats. Animal Behaviour 83, 1459-1468.

Topál, J., Miklósi, Á., Csányi, V., 1997. Dog-human relationship affects problem-solving behavior in the dog. Anthrozoös 10, 214-224.

Topál, J., Byrne, R., Miklósi, Á., Csányi, V., 2006. Reproducing human actions and action sequences: Do as I Do! in a dog. Animal Cognition, 9, 355-367.

Trinkel, M., Fleischmann, P.H., Steindorfer, A.F., Kastberger, G., 2004. Spotted hyenas *(Crocuta crocuta*) follow migratory prey. Seasonal expansion of a clan territory in Etosha, Namibia. Journal of Zoology 264, 125-133.

Troje, N.F., Huber, L., Loidolt, M., Aust, U., Fieder, M., 1999. Categorical learning in pigeons: The role of texture and shape in complex static stimuli. Vision Research 39, 353-366.

Tulving, E., 1972. Episodic and semantic memory. In: Donaldson, W., Tulving, E., (Eds.), Organization of memory. Oxford: Academic Press.

Tulving, E., 1985. Memory and consciousness. Canadian Psychologist 26, 1-12.

Tyack, P.L., 1997. Development and social functions of signature whistles in bottlenose dolphins *Tursiops truncatus*. Bioacoustics 8, 21-46.

Udell, M.A.R., Dorey, N.R., Wynne, C.D.L., 2008. Wolves outperform dogs in following human social cues. Animal Behaviour 76, 1767-1773.

Udell, M.A.R., Dorey, N.R., Wynne, C.D.L., 2010. The performance of stray dogs (*Canis familiaris*) living in a shelter on human-guided object-choice tasks. Animal Behaviour 79, 717-725.

Udell, M.A.R., Dorey, N.R., Wynne, C.D.L., 2011. Can your dog read your mind? Understanding the causes of canine perspective taking. Learning & Behavior 39, 289-302.

Van Parijs, S.M., Clark, C.W., 2006. Long-term mating tactics in an aquatic-mating pinniped, the bearded seal, Erignathus barbatus. Animal Behaviour 72, 1269-1277.

VanValkenburgh, B., Curtis, A., Samuels, J.X., Bird, D., Fulkerson, B., Meachen-Samuels,

J., Slater, G.J., 2011. Aquatic adaptations in the nose of carnivorans: evidence from the turbinates. Journal of Anatomy 218, 298-310.

Viranyi, Z., Gacsi, M., Kubinyi, E., Topal, J., Belenyi, B., Ujfalussy, D., Mi., 2008. Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). Animal Cognition 11, 373-387.

Vonk, J., Jett, S.E., Mosteller, K.W., 2012. Concept formation in American black bears, *Ursus americanus*. Animal Behaviour 84, 953-964.

Vonk, J., Johnson-Ulrich, Z., 2014. Social and nonsocial category discriminations in a chimpanzee *(Pan troglodytes*) and American black bears *(Ursus americanus*). Learning & Behavior 42, 231-245.

Wells, D.L., Hepper, P.G., 2003. Directional tracking in the domestic dog, *Canis familiaris*. Applied Animal Behaviour Science 84, 297-305.

West, B., Zhou, B.X., 1988. Did chickens go North? New evidence for domestication. Journal of Archaeological Science 15, 515-533.

Whitt, E., Douglas, M., Osthaus, B., Hocking, I., 2009. Domestic cats (*Felis catus*) do not show causal understanding in a string-pulling task. Animal Cognition 12, 739-743.

Wills, A.J., Lea, S.E.G., Leaver, L.A., Osthaus, B., Ryan, C.M.E., Suret, M., Bryant, C.M.L., Chapman, S.J.A., Millar, L., 2009. A comparative analysis of the categorization of multidimensional stimuli: I. Unidimensional classification does not necessarily imply analytic processing; evidence from pigeons (*Columba livia*), squirrels (*Sciurus carolinensis*) and humans *(Homo sapiens*). Journal of Comparative Psychology 123, 391-405.

Windholz, G., 1999. Protopopov's ideas on habit formation and their relation to the Pavlovian theory of higher nervous activity. American Journal of Psychology 112, 437-448.

Woodruff, G., Premack, D., 1979. Intentional communication in the chimpanzee: Development of deception. Cognition 7, 333-362.

Wright, A.A., Cook, R.G., Rivera, J.J., Sands, S.F., Delius, J.D., 1988. Concept learning by pigeons: Matching-to-sample with trial-unique video picture stimuli. Animal Learning and Behavior 16, 436-444.

Wyrwicka, W., 1994. Jerzy Konorski (1903-1973) on the 20th anniversary of his death. Neuroscience and Biobehavioral Reviews 18, 449-453.

Zaine, I., Domeniconi, C., Wynne, C.D.L., 2015. The ontogeny of human point following in dogs: When younger dogs outperform older. Behavioural Processes 119, 76-85.

Zamisch, V., Vonk, J., 2012. Spatial memory in captive American black bears (*Ursus americanus*). Journal of Comparative Psychology 126, 372-387.

- I5 - NEUROBIOLOGY OF EMPATHY. A LESSON FROM PRIMATES

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Keywords: *cognitive processes; contagion; empathy; mirror system; neurobiology*

Empathy has been considered for long a complex capacity involving mentalizing skills in order to understand the feelings, or thoughts, of another individual. The statement "I understand what you feel" seems to involve some mental capacity that connects the own experience with that of others. However, it is becoming evident that empathy is not a unitary process, but is a multilayered phenomenon in which emotions and cognitive processes can be simultaneously at work (de Waal, 2008; de Waal, 2012; Bernhardt & Singer, 2012). Instead of searching for a unified theory of empathy, several researchers have attempted to dissect it in its core elements and to understand its basic mechanisms in terms of neural underpinnings and cognitive processes. This bottom-up approach has been much more useful to understand empathy, as it provided a more comprehensive evolutionary perspective of the species that are endowed with some basic mechanisms responsible for empathic responses.

Several scholars agree that at the basis of empathic responses among several animal species, including humans, there is an emotional response that is shared between two or more individuals, named emotional contagion (Preston & de Waal, 2002). This phenomenon is probably based on an action-perception mechanism and is widespread among primates, and likely present in several other species of animals. I will also provide evidence that in rodents this mechanism is more common than previously thought.

Several behavioral phenomena involving emotional contagion have been investigated in human and nonhuman primates. They show that in highly social species, such as humans, macaques or gelada baboons, individuals tend to mimic the facial gesture of another individual. Very recently this phenomenon has also described in dogs, showing that it could be much more widespread, especially in species with robust face-to-face communication. This behavioral matching seems to play an important role in connecting the own experience with that of others. These phenomena are particularly contagious as individuals can hardly refrain from responding. One of these behaviors is yawning. Studies in geladas and humans showed that the level of contagious is correlated with the quality of the relationship between individuals, suggesting that there is a link between contagious behaviors and interpersonal emotional connection.

The capacity to mimic others' behaviors and emotions seems to stem from an ancient evolutionary capacity that is already present very early in primate development. For example, human, ape, and monkey neonates are capable of imitating facial gestures displayed by a human model (Meltzoff & Moore, 1977; Ferrari et al., 2006). This capacity probably evolved to tune an infant's behavior to that of the mother, thus facilitating the mother-infant relationship and imitative exchanges (Christov-Moore et al., 2014). It is therefore not surprising that, according to several authors, the building blocks of empathy may be found in the early mother-infant relationship (de Waal, 2008; Decety, 2011).

From a neurobiological point of view, empathy has been widely investigated in its most basic components, but also in the cognitive processes that may modulate it. One of the basic mechanism of empathy involves the possibility to activate shared cortical representations to directly experience and interpret others' behavior. In particular the discovery of mirror neurons or of a similar mechanism in different primate species (Macaques, chimpanzees, marmosets and Humans) has been particularly stimulating. Mirror neurons have been

described in premotor and posterior parietal cortices, and they fire both when a specific action is observed and when the same action is performed by another individual. The fact that MN have been found in cortical areas involved in motor control, has led to the proposal that others' actions can be translated into a motor code exploiting the inner knowledge, in terms of cortical motor representations of the individual. This translation allows an individual to map others' actions/emotions onto the internal motor representation of that action/emotion. The possibility that a mirror mechanism is involved in empathy has been supported by several investigations showing that they fire during production and observation of facial gestures in both macaques and humans. In addition the observation of emotional facial gestures also activates areas that are part of circuits involved in emotional responses, such as the insular cortex and the anterior cingulate cortex, and the visceral reactions associated to them (Singer & Heit, 2012). Lastly, the mirror system has been demonstrated to be involved in imitation, thus supporting the capacity to express emotions after they have been observed in other individuals.

Despite some forms of empathy require a direct activation of body shared representations, other forms rely on more cognitive mechanisms. There is a cognitive route in which individuals can evaluate the social situation without necessary sharing the emotional state of others. This is especially useful when, for example, individuals make decisions about how to respond in a situation in which their own behavior could be risky for their own survival (e.g. supporting a companion in a physical conflict with a competitor). Often individuals show a feeling of concern for the other and wishes to increase the other's welfare. In these cases, the empathic mirroring response would be useful for understanding the emotions of others, but the appropriate response should take into account important aspects of the context, with an accurate evaluation of costs and benefits as consequences of one's decision. Under these circumstances the brain must integrate several pieces of information regarding previous experiences, including the risks and advantages of an action, and it should assign values to others' behaviors or to their own responses (Shamay-Tsoory et al., 2009; Forbes & Grafman, 2010). These studies, carried out mainly in human with neuroimaging tools, have individuated a series of brain areas which are part of the mentalizing network, involving medial prefrontal cortex and the temporoparietal junction (TPJ).

References

Christov-Moore, L., Simpson, E.A., Coudé, G., Grigaityte, K., Iacoboni, M., Ferrari, P.F., 2014. Empathy: Gender effects on brain and behavior. Neurosci Biobehav Rev 46, 604-627.

Decety, J., 2011. The neuroevolution of empathy. Ann N Y Acad Sci 1231, 35-45.

de Waal, F.B., 2008. Putting the altruism back into altruism: the evolution of empathy. Annu Rev Psychol 59, 279-300.

de Waal, F.B., 2012. The antiquity of empathy. Science 336, 874-876.

Ferrari, P.F., Gallese, V., Rizzolatti, G., Fogassi, L., 2003. Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. Eur J Neurosci 17, 1703-1714.

Ferrari, P.F., Visalberghi, E., Paukner, A., Fogassi, L, Ruggiero, A, Suomi, S.J., 2006. Neonatal imitation in rhesus macaques. PLOS Biol 4, 1501-1508.

Lamm, C., Decety, J., Singer, T., 2010. Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. Neuroimage 54, 2492-2502.

Meltzoff, A.N., Moore, M.K., 1977. Imitation of facial and manual gestures by human neonates. Science 198(4312), 75-78.

Preston, S.D., de Waal, F.B., 2002. Empathy: Its ultimate and proximate bases. Behav Brain Sci 25, 1-20.

Shamay-Tsoory, S.G., Aharon-Peretz J., Perry, D., 2009. Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus

ventromedial prefrontal lesions. Brain 132, 617-627.

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R.J., Frith, C.D., 2004. Empathy for pain involves the affective but not sensory components of pain. Science 303, 1157-1162.

Singer, T., Heit, G., 2012. Human empathy through the lens of psychology and social neuroscience. In: de Waal, F.B., Ferrari, P.F., (Eds.), The Primate Mind Harvard University Press, Cambridge, 158-174.

- I6 - PERCEPTION AND PROCESSING OF FACIAL INFORMATION IN DOGS

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Abstract:

Visual cues from faces provide important information about an individual's identity, affective state, intention, cognitive activity, and temperament. The ability to recognize these cues and to respond promptly and appropriately guides effective human social interactions. Although dogs are distantly related to humans phylogenetically, the structure of their visual system does not impose serious limitations on the use of visual cues for social cognition and interaction. In fact, recent studies have revealed remarkable similarities in the ways that faces are perceived and processed in humans and dogs. This review will summarize what we have learned so far about face perception (e.g., face identity, facial expression) in dogs. It will also try to highlight the challenges we are currently facing in order to understand cognitive and neural mechanisms underlying dogs' social cognition.

Keywords: *dogs; emotion; face; gaze behaviour; social cognition*

Introduction

Faces are probably the most important visual stimuli in our social environment. They not only provide visual information about an individual's gender, age and familiarity, but can also communicate significant cues to affective state (e.g., happy), intention (e.g., gaze direction), cognitive activity (e.g., concentration), and temperament (e.g., hostility). In humans, the processing of these complex facial cues seems to involve a face-specific cognitive and neural mechanism (Bruce & Young, 2012).

Considering that the use of visual cues for recognizing individuals and their emotional states has clear advantages over olfactory (e.g., need to be highly proximal) and auditory cues (e.g., dependent on whether an individual vocalizes or not), the capacity to read faces is not restricted to humans, and can be found extensively in other social species. Although domestic dogs (*Canis familiaris*) have comparatively lower visual acuity, less binocular overlap, less range of accommodation and limited colour perception (dichromatic color vision) in comparison with humans (Miller & Murphy, 1995), their visual system and brain structure does not impose serious limitations on the use of visual cues for social cognition. Interestingly, probably due to their unique history of domestication and selective breeding, they are unusually skilled, in some cases even more so than non-human primates, at reading human social-communicative signals which may represent a case of convergent cognitive evolution (Hare & Tomasello, 2005).

In this review, I will summarize empirical evidence mainly from behavioural and eye-tracking studies in our group to show dogs' capability of sampling and processing several facial cues (e.g., facial identity, facial expression), and illustrate the extraordinary similarities in face processing strategy between humans and dogs. However, due to various technical and ethical challenges, little is known about the neural mechanisms underlying face perception in dogs.

Perceiving face identities

Humans are highly efficient at differentiating and identifying human faces, possibly through a holistic or configural process in which we perceive relations among individual facial features (e.g., eyes, nose and mouth) and then integrate all features into a single representation

of the whole face (Bruce & Young, 2012). This configural processing is often assessed by the face-inversion effect, defined as a larger decrease in recognition performance for faces than for other single-oriented objects when they are presented upside-down. Such face-inversion effect is likely caused by a disruption in the processing of orientation-sensitive facial configural information (Bruce & Young, 2012).
Dogs can also use visual cues alone to perceive face identity information presented in black-and-white pictures, possibly through inversion-sensitive configural process (Racca et al., 2010). In a visual paired comparison (preferential looking) procedure, dogs showed a clear viewing preference by looking longer at a novel human face image when simultaneously presented with a prior-exposed familiar human face. For a pair of dog faces, however, they tended to fixate longer at a familiar dog face when paired with a novel dog face, suggesting dogs can use species-specific facial cues alone to differentiate individual dogs and humans. Interestingly, no significant looking preference was detected for inverted human or dog face images, implying that dogs may also use a human-like configural strategy in face identity perception (Racca et al., 2010). However, it is unclear how well dogs can visually differentiate individuals' faces from conspecifics or heterospecifics, whether they show experience-related face recognition bias (e.g., own-race bias in humans), whether they form an internal representation of 'average face' for face discrimination and recognition, and the contribution of internal and external facial features in face identity recognition.

Perceiving facial expressions

In addition to face identity, humans show very high perceptual sensitivity to facial expressions of emotion, especially those representing our typical emotional states such as happiness, sadness, fear, anger, disgust, and surprise. We can categorically discriminate these expressions even with very brief face presentation (<100ms) or when focal attention is not fully available (Bruce & Young, 2012).
Over the last few years, there is growing evidence to suggest that pet dogs are sensitive to human emotions and are able to use some facial expression cues to guide their actions (Hare & Tomasello, 2005). They can visually discriminate human smiling faces from blank faces (Nagasawa et al., 2011), and can selectively respond to happy or angry human facial expressions using configural facial cues (Müller et al., 2015). For instance, when trained with only half of a unfamiliar human face (e.g., the lower mouth region of a happy face or the upper eye area of an angry face), dogs could generalized the learned discrimination to the other half of the face displaying the same expression, indicating they may use memory of real emotional human faces to accomplish this discrimination task (Müller et al., 2015). However, these human-expression-modulated behavioural responses could be attributed solely to learning of contiguous visual features. Dogs might be discriminating human facial expressions without 'understanding' the transmitted emotional information.
Recently through a cross-modal preferential looking paradigm, we conclusively demonstrated that dogs possess at least the mental prototypes for emotional categorization, such as positive versus negative affect (Albuquerque et al., 2016). When two human or dog faces with different emotional valences (happy/playful versus angry/aggressive) were presented side-by-side and paired with a single vocalization from the same individual with either a positive or negative valence, dogs looked significantly longer at the face whose expression was congruent to the valence of vocalization, for both conspecifics and heterospecifics, an ability previously known only in humans. This spontaneous viewing preference did not require behavioural training and was not constrained by the familiarity of face identity and vocalization language. Our results demonstrate that dogs can extract and integrate bimodal sensory emotional information, and visually discriminate between positive and negative emotions from both human and dog faces. Future research could investigate how fine these categorical emotion representations are in dogs' mind, and whether they would respond accordingly to different emotion categories.

Cognitive bias in face processing

Probably due to the right hemisphere advantage in face processing, humans are more likely to use facial cues contained in the right side of the owner's face (left side from viewer's perspective) to facilitate perceptual judgement of facial information, such as gender, identity, expression, and attractiveness. This left perceptual bias in face perception is often accompanied by a left gaze bias (LGB), in which the left hemiface is often inspected first and/or for longer periods (Guo et al., 2012). Considering that 6-month-old infants only show a general, inherent LGB for both face and non-face object images, which later transforms itself into a specific LGB for face images only as demonstrated in 4-year-old children and adults (Guo et al., 2009; Racca et al., 2012), the face-related LGB in humans seems to be an acquired behaviour, possibly through the process of experience-dependent gradual specialization during development.

Using a preferential looking protocol and with the presentation of neutral human, monkey and dog face images, we have found that pet dogs demonstrated both initial and overall LGB only for human faces, but not for monkey or dog faces, nor for inanimate object images (Guo et al., 2009). Such face-specific and species-sensitive gaze biases may have significant adaptive value and could be linked to dogs' unique evolutionary and ontogenetic history. For pet dogs, the ability to extract information from human faces and to respond appropriately could have had a selective advantage during the process of domestication, especially as the emotional content of these faces may have immediate adaptive behavioural significance. The lack of LGB in viewing of monkey and dog faces might reflect a reduced need or sensitivity in assessing these faces with neutral facial expressions, although the differentiating criteria remain to be established. Interestingly, although to a less degree, a group of human-raised wolves also presented initial LGB towards human faces, but not towards wolf faces or objects. On the other hand, the hunting hounds did not show any directional head turning bias when exploring human faces, dog faces and object images (unpublished data). It seems that enculturation (ontogenetic exposure), rather than domestication (phylogenetic exposure), plays a more crucial role for *Canis* species to establish a LGB in processing human faces. This exposure-bias adaptation hypothesis could be examined thoroughly in future research with a comparable methodology and larger sample size.

To further understand whether the LGB in dogs is an automatic reflection of hemispheric lateralization in face processing, or is associated with the perceptual processing of a specific type of facial information, Racca et al. (2012) presented dog and human faces with different emotional valences (negative: threatening or anger; neutral; positive: friendly or happy) to pet dogs, and observed a consistent LGB for negative and neutral human facial expressions, but no bias for positive expressions. Perhaps dogs interpret human neutral facial expressions as potentially negative, given their lack of clear approach signals. They, however, demonstrated a differential gaze asymmetry for dog faces based on their emotional valence, with no gaze bias for neutral expressions but a LGB for negative expressions and a right gaze bias (RGB) for positive expressions (Racca et al., 2012). These observations are broadly consistent with the Valence Model of cerebral lateralization in emotion processing, with the left and right hemisphere mainly involved in the processing of positive and negative emotions, respectively. It should be noted that the Valence Model is one of current available psychological theories in emotion perception and may present a simplified view of emotional processing.

In comparison with human and non-human primates, it seems that gaze asymmetry in pet dogs is a reflection of brain lateralization not only in face perception but also in emotion processing. Dogs present differential lateralized eye movements depending on the species and the emotional valence of the face viewed, such as a clear LGB for human and dog faces with negative emotional valence, a RGB for dog faces with positive emotional valence (Racca et al., 2012), and no bias for monkey faces (Guo et al., 2009). Although it could be argued that the gaze bias in dogs might be a simple response to potential reward/punishment or

approach/avoidance behaviour and is not necessarily correlated with human-like emotion perception or experience, such observations imply a broader adaptive value of this natural gaze asymmetry in domestic dogs.

Cognitive and neural mechanisms in face processing

When exploring a face, humans tend to adopt a 'holistic' viewing strategy to selectively integrate local facial information from key internal facial features (i.e. eye, nose, and mouth) into a single representation of the whole face (Guo, 2012). Regardless of the ongoing perceptual task demands (e.g., free viewing, face learning, identity judgement, facial expression categorization) and face species (e.g., human, monkey, dog, and cat faces), we direct the majority of fixations at the eye region, followed by the nose and mouth (Guo et al., 2010, 2012; Gavin et al., 2016), suggesting a crucial role of the eyes in transmitting various elements of facial information and possibly a generic "built-in" scanning strategy in our brains for general face processing (Guo, 2012).

In canine cognition research, the common research techniques, such as preferential looking, often lack spatial accuracy, permitting only gross judgments of the location of the dog's gaze point and are limited to a laboratory setting. Recently, researches have started to adapt head-mounted or remote video-based eye-tracking systems to study naturalistic viewing behaviour with a higher level of spatial accuracy in dogs (Williams et al., 2011). By applying these new systems to examine dogs' gaze allocation in face perception, researchers have noticed that like humans, dogs prefer to fixate more at the internal facial features (especially at the eyes) when viewing human and dog faces (e.g., Somppi et al., 2014). Future studies could make comprehensive across-species comparisons to examine how dogs extract diagnostic local facial cues and use them to guide or facilitate different behavioral tasks, such as emotion recognition.

Regarding the neural mechanism underlying face perception, brain imaging studies have revealed a face-specific cortical processing system in humans, such as a distributed network of brain structures, including the fusiform gyrus, associated with face processing (Bruce & Young, 2012). After training dogs to remain awake, still and unrestrained inside an MRI scanner, Cuaya et al. (2016) compared brain activity elicited by human faces against everyday objects in dogs, and found enhanced brain activity to face stimuli in several cortical regions in the bilateral temporal cortex. This localised 'face-sensitive' area within the temporal lobe (e.g., fusiform face area in humans) has been consistently reported in sheep, monkeys and humans, implying a high degree of evolutionary conservation of this brain region for face processing.

Conclusion

Although dogs are not strictly diurnal or nocturnal species and are considered as "visual generalists" (Miller & Murphy, 1995), they can rely on visual cues alone (e.g., 2D black-and-white pictures) to perceive and discriminate face identity and emotional information. Even phylogenetically dogs are relatively distant from humans, the visual system of these two species are tuned to the same visual cues for processing (at least) social scenes. That is, dogs have demonstrated clear human-like visual preference and cognitive bias in face perception. The many shared features of face processing among these two species suggest that face perception may have evolved to suit the needs of complex social communication and interaction. Furthermore, studying the presence or the absence of a human-like face-processing behaviour in dogs, in light of knowledge of their socio-ecological constraints, can provide information regarding the evolutionary connection and selective pressures leading to the emergence of the face processing system.

Current research on canine cognition mainly relies on behaviour observation and measurements. We know very little about the structure of visual system and functional connectivity between different cortical regions inside dogs' brain. With the increasing availability of many non-invasive measures, such as eye-tracking, electroencephalography,

electromyography and functional magnetic resonance imaging, it is now possible for researchers to adopt a combined approach to assess dogs' cognitive abilities, and systematically study the role of facial communication in human-dog interactions and its underlying cortical mechanisms.

References

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., Mills, D., 2016. Dogs recognize dog and human emotions. Biol Lett 12, 20150883.

Bruce, V., Young, A.W., 2012. Face perception. London: Psychology Press.

Cuaya, L.V., Hernández-Pérez, R., Concha, L., 2016. Our faces in the dog's brain: functional imaging reveals temporal cortex activation during perception of human faces. PLOS One 11(3), e0149431.

Gavin, C.J., Houghton, S., Guo, K., 2016. Dog-owners show experience-based viewing behavior in judging dog face approachability. Psychol Res 1-8.

Guo, K., Meints, K., Hall, C., Hall, S., Mills, D., 2009. Left gaze bias in humans, rhesus monkeys and domestic dogs. Anim Cogn 12, 409-418.

Guo, K., Tunnicliffe, D., Roebuck, H., 2010. Human spontaneous gaze patterns in viewing of faces of different species. Perception 39, 533-542.

Guo, K., 2012. Holistic gaze strategy to categorize facial expression of varying intensities. PLOS One 7(8), e42585.

Guo, K., Smith, C., Powell, K., Nicholls, K., 2012. Consistent left gaze bias in processing different facial cues. Psychol Res 76, 263-269.

Hare, B., Tomasello, M., 2005. Human-like social skills in dogs. Trends Cogn Sci 9, 439-444.

Miller, P.E., Murphy, C.J., 1995. Vision in dogs. J Am Vet Med Assoc 207, 1623-1634.

Müller, C.A., Schmitt, K., Barber, A.L.A., Huber, L., 2015. Dogs can discriminate emotional expressions of human faces. Curr Biol 25, 601–605.

Nagasawa, M., Murai, K., Mogi, K., Kikusui, T., 2011. Dogs can discriminate human smiling faces from blank expressions. Anim Cogn 14, 1–9.

Racca, A., Amadei, E., Ligout, S., Guo, K., Meints, K., Mills, D., 2010. Discrimination of human and dog faces and inversion responses in domestic dogs (Canis familiaris). Anim Cogn 13, 525-533.

Racca, A., Guo, K., Meints, K., Mills, D.S., 2012. Reading faces: differential lateral gaze bias in processing canine and human facial expressions in dogs and 4-year-old children. PLOS One 7(4), e36076.

Somppi, S., Törnqvist, H., Hänninen, L., Krause, C. M., Vainio, O., 2014. How dogs scan familiar and inverted faces: an eye movement study. Anim Cogn 17, 793-803.

Williams, F., Mills, D., Guo, K., 2011. Development of a head-mounted, eye-tracking system for dogs. J Neurosci Methods 194, 259-265.

- I7 - CHASING RAINBOWS: FACTORS AFFECTING THE DOG-HUMAN RELATIONSHIP

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Abstract:

Any assumption that there is such a thing as 'the' dog-human relationship can be quickly dispelled by a cursory glance at the literature in this field. Nonetheless, it is instructive for both scientists and those who work with dogs to consider factors shown to affect dog-human relationships. Doing so might enable practitioners to more closely match dogs and humans together, with benefits for members of both species. In addition, scholars can potentially learn much about the nature of relationships per se. In this paper, dog and human factors known to affect dog-human relationships are reviewed. While many factors have been identified, ranging from dog behavioral traits through to human personality traits, it is argued that effect sizes are generally small and that merely cataloging these factors is intellectually unsatisfying. What may be required instead are two shifts in thinking. First, while theories derived from human-human relationship research, such as attachment theory, may be applicable to dog-human relationships, developments in evolutionary theory mean that their use requires justification. Alternative theories which are inherently interspecific should also be developed and considered. Second, a focus on individual dog or human factors may be less rewarding than a focus on the dog-human system. Family systems theory holds that, in open systems such as interpersonal relationships, many beginnings can result in the same outcome and the same beginnings can result in diverse outcomes. A critical undertaking, therefore, is understanding how communication between participants leads to circular positive and negative feedback loops that establish general patterns of behavior within the system. A family systems approach might allow us to see individual dog-human relationships as something more than aggregations of human and dog characteristics. A challenge, therefore, is to incorporate into the field of anthrozoology this more complex level of social analysis.

Keywords: *anthrozoology; dog-human relationships; family systems theory*

Introduction

Consider the following excerpts. In the first, a successful business consultant in a large Australian city describes how his relationship with his companion dog, Tiberius, differs from his relationships with people. In the second, an Australian farmer describes his sheepdog Jock.

"There is never really a time when you don't have that same level of love for him or the same sort of closeness with him. If he does something bad, like bark at the neighbor or something like that, that's only a fleeting thing and you'll still pick him up and hug him. I guess that's a difference between human relationships and relationships with dogs. I guess there are times when I do things to upset other people as well. With Tiberius it's different; you don't have that same sort of problem. He never gets upset with me." (extract from Schaan, 2011, pp. 191).

"He seemed to know exactly what was needed and, by the age of six months, was an almost perfect sheepdog. For nearly sixteen years he performed almost everything expected of him… Jock never slept in a house or shed or drum or kennel. Even in old age and in mid-

winter, he would still sleep flat out on his side in the middle of the yard. It was not uncommon to go out on a frosty morning and find him snow-white, covered in frost, and as stiff as a board. I would pick him up and prop him against the silo on the sunny side. He would slowly move around it, following the sun, until he had thawed out enough to walk away for a feed and drink and a look at the sheep yards to see if anything was happening. One cold day he did not thaw out. We had lost the best friend and helper our family ever had." (extract from Goode & Hayes, 1998, pp. 131).

These excerpts illustrate two important things about dog-human relationships. First, both tell of a relationship that is, or was, extremely meaningful to the humans involved. Tiberius lives the life of a contemporary urban companion animal. His owner reports that '*there is never really a time when you don't have that same level of love for him*' Jock worked hard and died alone, without ceremony. He is described as '*the best friend and helper our family ever had*'. Second, any assumption that there is such a thing as 'the' dog-human relationship is impossible to justify. Attempts to identify even broad functional categories – companion dog, detection dog, farm dog, vermin; owner, guardian, handler, trainer – are unsatisfactory. Categories overlap. Within them, diversity outweighs uniformity.

Despite this, it is instructive to reflect on factors that affect dog-human relationships. Doing so might enable practitioners to more closely match dogs and humans together, with clear benefits for members of both species. In addition, scholars could potentially learn much about the nature of relationships per se, including those that involve people from different generations, countries, religions or cultures, or those between humans and other animal species, many of which face extinction without human intervention. The hyper-social, globally interconnected nature of our modern existence makes understanding and improving relationships a central issue for us all.

But what exactly does the term 'relationship' mean? According to Jackson-Dwyer (2013) one definition from human psychology holds that a relationship exists to the extent that two people exert strong, frequent and diverse effects on one another over an extended period of time. This anthropocentric definition is clearly inadequate! In her book, Jackson-Dwyer (2013) describes three factors that characterize close human-human relationships: interdependence, need fulfilment and emotional attachment. These are not features of all dog-human relationships, clearly excluding those that are purely functional or devoid of emotional attachment. They are, however, features of the types of dog-human relationships that currently attract the majority of research interest, particularly in developed Western cultures. Most dogs in contemporary societies are kept primarily for companionship. Most are described as family members. Taking this into consideration, we might conclude that *an interpersonal relationship exists between a human and a dog to the extent that these two agents interact directly with each other in ways involving interdependence, need fulfilment and emotional attachment, and to the extent that they exert strong, frequent and diverse effects on one another.* This definition is also imperfect, but it allows us to begin to consider what factors might affect such relationships.

Evolution as a factor affecting dog-human relationships

Evolutionary theory easily accounts for intraspecific affiliative tendencies in domestic dogs (Kubinyi et al., 2007) and modern humans (Jackson-Dwyer, 2013). Indeed, leading theorists argue that the need to belong to a social group is a fundamental human motivation, almost as compelling as needs for food, water and shelter (Maslow, 1987; Baumeister & Leary, 1995). Cross-species affiliations are more challenging to explain (Herzog, 2014). Some authors contend that individual persons are attracted to dogs emotionally because humans' powerful, intraspecific affiliative tendencies are hijacked by dog features that may have evolved because of this very effect, which presumably enhanced reproductive opportunities for some dogs over others (Archer, 2011). Others, such as Shipman (2010), argue instead that affiliative dog-human relationships may have been of great evolutionary importance in their own right.

This unresolved debate is an important one. If the psychological mechanisms underlying interspecies relationships are identical to, indeed hijacked from, those underlying intraspecific relationships, then theories derived from human psychology, such as attachment theory, are likely to apply, as are those derived from canine ethology. This might explain positive correlations between owner preferences for cute features and their self-reported strength of attachment to their companion animal (Archer & Monton, 2011), as well as popular models of dog training claimed to be based on pack theory (Millan, 2007). Certainly, many authors have used attachment theory to inform studies of dog-human relationships. If, however, interspecific relationships evolved alongside, but independently from, intraspecific ones, then entirely different psychological mechanisms may underlie their development, maintenance and, sometimes, their disintegration. This might explain why some people, perhaps even some cultures, are captivated by dogs or human infants, but not both, and also why some dogs are highly sociable towards other dogs, but not people, and vice versa. Dissociations such as these are worthy of further research. Their existence might indicate a need for a paradigm shift in this field. Instead of conducting further studies drawing on existing theories, it may be necessary to develop entirely new, inherently interspecific, replacements.

Dog factors affecting dog-human relationships

Individual humans sometimes form close relationships with unusual things, such as pet rocks, robots and electronic devices. Close relationships with animals are particularly frequent, however, and close relationships with dogs most frequent of all. To some extent, this is likely due to dog biology. Human infants are prepared from birth to recognize human faces (Turati et al., 2008) and form relationships with familiar people. Indeed, humans have evolved a specialized face-processing module in the brain to facilitate facial recognition (Kanwisher, 2010). Recent research suggests that dogs may possess an analogous brain region (Cuaya et al., 2016). This may underlie some of the impressive social cognitive skills demonstrated by dogs and reviewed elsewhere (Kaminski & Marshall-Peschini, 2014). Particularly relevant to dog-human relationship formation and maintenance, are studies showing that dogs are very good at discriminating visually between two humans (Huber et al., 2013). They are also adept at detecting and responding to visual information about human attentional (Gácsi et al., 2004) and emotional (Nagasawa et al., 2011) states. Human children are likewise very attuned to living organisms and may be predisposed to develop relationships with animals (Melson, 2001).

Species-wide predispositions explain why dogs and humans readily form relationships, but do not account for individual differences within these relationships. Yet dozens of studies affirm that relationships do differ, and that they are greatly affected by characteristics of individual dogs. When Australian adults were asked to describe their ideal companion dog, the most strongly endorsed attributes were behavioral (King et al., 2009). Similar results were recently obtained in a sample of Italian adults (Diverio et al., in press). It is also well established that undesirable dog behaviors are one of the main reasons why dogs are relinquished to shelters (Marston & Bennett, 2003). Individual differences in behavior reflect a combination of genetics and developmental experiences. Numerous studies, reviewed in Serpell and Duffy (2014)and Mehrkam and Wynne (2014), have documented breed differences in social behaviors likely to be relevant to human-dog relationships. Within-breed differences are also substantial, particularly when breeding goals have led to the development of distinct genetic lines within a breed. The effects on adult behavior of specific experiences during early developmental periods were documented by Scott & Fuller (1965). While difficult to disentangle without compromising the welfare of experimental animals, subsequent studies have largely confirmed the importance of appropriate socialization and training experiences in preparing dogs for life as human companions (Howell et al., 2015).

Dogs' physical appearance also affects dog-human relationships. In one recent study, 668 dog owners completed two relationship quality surveys and rated their dog's personality

and physical cuteness (Thorn et al., 2015). Personality measures and cuteness ratings predicted each measure of relationship quality, with cuteness ratings being the strongest unique predictor in three of seven models. McGreevy et al., (2004) report that dogs' eyes vary substantially in size, shape and structure and that this structural variation is associated with skull length and cephalic index. On this basis, it was proposed that flat-faced dogs, with large, round, forward-facing eyes, may be better able to focus on proximate human faces than other dogs, and that this may lead to greater success as human companions. If these physical features are associated with perceived cuteness, this may explain the relationship observed by Thorn et al., (2015). One way to test this proposal would be to compare brachycephalic and dolichocephalic dogs on dog-human relationship measures and measures of cuteness.

Human factors affecting dog-human relationships

Literature documenting human factors affecting dog-human relationships is prolific and difficult to summarize. Gender differences are commonly reported, as are differences due to personality characteristics, attitudes, age, family circumstances, personal history, and attachment style (Bennett & Rohlf, 2007; Meyer & Forkman, 2014). Humans are far more likely to form relationships with people with whom they share a house, a job, a schoolroom or some other physical space (Jackson-Dwyer, 2013). While this is unsurprising, it was found in a recent study that human-dog relationships were also influenced by how much time the participants spent together (Bennett et al., 2015). This may explain why many studies fail to find differences between dog owners and non-owners on critical variables. Ownership per se is likely to be far less important than the amount of time spent in close proximity or devoted to shared activities.

Surprisingly little attention has been paid to social and cultural factors affecting dog-human relationships. Jegatheesan (2012) described a number of reasons why such studies are difficult to conduct and interpret. One of the challenges is understanding what different cultures mean when they use common terms. For example, while it is often reported that pets are considered to be family members, the concept of 'family member' is rarely defined. In cultures where the term refers to a large kin group, with whom the person in question may have no direct interpersonal contact, the pet dog may be described as a 'family member', but perform roles not typically associated with this label by the academic community. Disentangling these functions is extremely difficult without a thorough linguistic analysis.

In an interesting study which used culturally appropriate methods to examine human-dog relationships in rural and remote indigenous communities in Australia, Constable et al., (2010) found that dogs were highly valued. Positive attitudes towards dogs were often linked with traditional values and beliefs, including beliefs concerning close kinship between animals and humans. Individual relationships between people and specific dogs were prevalent, although dogs typically wandered unchecked and in large groups in these communities. Many experienced very poor health and a lack of fertility control was associated with overpopulation and associated problems such as nuisance barking, biting and property destruction. Indiscriminate shooting and poisoning of dogs presumed by authorities to be stray were, nonetheless, widely condemned. As one respondent commented "*…a lot of people really like their dogs around here, scabby as they are, you try and take them and they lock them in the cupboards, hide them in the bathroom.*"

Where to next – family systems theory?

Although many factors affect dog-human relationships, there is something unsatisfying about simply cataloging these effects, particularly when effect sizes are small or when multiple factors are tested and only a few found to be significant. To drive the field forward requires theoretical development. Should dog-human relationships be studied using theories derived from human-human relationship research? If so, exactly which theories are applicable and what role or roles might the dog be expected to play? Is the owner a

parent, friend, lover, spouse, sibling or child? Some scholars have tackled this issue (Blouin, 2012) but there is scope for much more work. Perhaps human-human theories do not map well onto dog-human relationships at all, and entirely new anthrozoological theories are required. If so, what might these look like?

One of the major theoretical approaches to understanding human relationships is Family Systems Theory or FST (Bavelas & Segal, 1982). From the perspective of FST, an individual family member can never be understood in isolation, but must be considered as one part of an interconnected, ecological system. This is important because such systems are not simply the sum of their component parts and they cannot be understood by analysis or deconstruction of these component parts. Instead, the FST analyst focuses on how the various components are interconnected and how a change in one component can affect other components, which then, in turn, affect the initial component in an iterative manner. Instead of looking for linear, cause-effect relationships, then, the focus is on interconnected patterns of communication and influence (International Encyclopedia of Marriage and Family, 2003).

FST has several premises which may further understanding of factors affecting dog-human relationships. First, it is understood that family systems are comprised of individual members who share a history and have some degree of emotional bonding. Second, while family systems are open rather than closed, their boundaries shifting as members interact with other people and the broader environment, it is expected that the system as a whole will typically develop strategies for meeting the needs of both individual members and the family. FST is committed to the principle of equifinality, which holds that, in open systems, many beginnings can result in the same outcome, while the same beginnings can result in diverse outcomes. There is also a commitment to examining patterns of communication between members, required to establish and maintain the system. According to Bavelas & Segal, (1982) all behavior within a family system is essentially, or at least potentially, communicative, revealing not only specific information (I want you to sit Daisy) but also information about the relationship (I am in a position where I can instruct you to sit).

From this perspective, a dogs' genetic predisposition to behave in a certain way never leads directly to expression of this behavior. Nor does the personality of a dog owner ever directly cause a dog to respond in a certain way. Instead, the owner's attributes interact with the dog's attributes and with the attributes of the environment in feedback and feedforward loops that establish general patterns of behavior within the dog-human system which allow that system to function more or less effectively within its ecological niche. Negative feedback loops maintain stability. Positive loops create change over time. Does Daisy sit when instructed to do so? This will depend on Daisy's characteristics, her owner's characteristics, their shared history, the current circumstances, and the nature of the ongoing relationship between both participants.

The promise of an FST approach is that it will allow researchers to see individual dog-human relationships as something more than an aggregation of human and dog characteristics, all of which have some, but perhaps not much, effect on the relationship. Cataloging factors affecting dog-human relationships is an important first step, but the real challenge in this field is to incorporate a more complex and sophisticated level of social analysis into a deep understanding of relationships that are both interpersonal and interspecies.

References

Archer, J., 2011. Pet keeping: A case study in maladaptive behavior, The Oxford handbook of evolutionary family psychology, Oxford University Press, New York, USA, 281-296.

Archer, J., Monton, S., 2011. Preferences for infant facial features in pet dogs and cats. Ethology 117, 217-226.

Baumeister, R.F., Leary, M.R., 1995. The need to belong: Desire for interpersonal attachments as a fundamental human motivation. Psych Bull 117, 497-529.

Bavelas, J.B., Segal, L., 1982. Family systems theory: background and implications. J

Commun 32, 99-107.

Bennett, P.C., Rohlf, V.I., 2007. Owner-companion dog interactions: Relationships between demographic variables, potentially problematic behaviours, training engagement and shared activities. Appl Anim Behav Sci 102, 65-84.

Bennett, P.C., Trigg, J.L., Godber, T., Brown, C., 2015. An experience sampling approach to investigating associations between pet presence and indicators of psychological wellbeing and mood in older Australians. Anthrozoös 28, 403-420.

Blouin, D.D., 2012. Understanding relations between people and their pets. Sociol Comp 6, 856-869.

Constable, S., Dixon, R., Dixon, R., 2010. For the love of dog: the human–dog bond in rural and remote Australian indigenous communities. Anthrozoös 23, 337-349.

Cuaya, L.V., Hernández-Pérez, R., Concha, L., 2016. Our faces in the dog's brain: functional imaging reveals temporal cortex activation during perception of human faces. PLOS One 11, e0149431.

Diverio, S., Boccini, B., Menchetti, L., Bennett, P.C. . The Italian perception of the ideal companion dog. J Vet Behav: Clin Appl Res (in press).

Gácsi, M., Miklósi, A., Varga, O., Topál, J., Csányi, V., 2004. Are readers of our face readers of our minds? Dogs (Canis familiaris) show situation-dependent recognition of human's attention. Anim Cogn 7, 144-153.

Goode, A., Hayes, M., 1998. The complete book of great working dog stories. ABC Books, Sydney, Australia.

Herzog, H.A., 2014. Biology, culture, and the origins of pet-keeping. Anim Behav Cogn 1, 296.

Howell, T.J., King, T., Bennett, P.C., 2015. Puppy parties and beyond: the role of early age socialization practices on adult dog behavior. Vet Med: Res Rep 6, 143-153.

Huber, L., Racca, A., Scaf, B., Virányi, Z., Range, F., 2013. Discrimination of familiar human faces in dogs (Canis familiaris). Learn Motiv 44, 258-269.

International Encyclopedia of Marriage and Family, 2003. Family Systems Theory, Retrieved April 09, 2016 from Encyclopedia.com: http://www.encyclopedia.com/doc/1G2-3406900166.html

Jackson-Dwyer, D., 2013. Interpersonal Relationships. Taylor & Francis.

Jegatheesan, B., 2012. Using an adaptive methodology to study human–animal interactions in cultural context. Anthrozoös 25, 107-121.

Kaminski, J., Marshall-Peschini, S., (Eds.), 2014. The social dog: behavior and cognition. Academic Press, San Diego, CA.

Kanwisher, N., 2010. Functional specificity in the human brain: A window into the functional architecture of the mind. Proc Natl Acad Sci U.S.A. 107, 11163-11170.

King, T., Marston, L.C., Bennett, P.C., 2009. Describing the ideal Australian companion dog. Appl Anim Behav Sci 120, 84-93.

Kubinyi, E., Virányi, Z., Miklósi, Á., 2007. Comparative social cognition: from wolf and dog to humans. Comp Cogn Behav Rev 2, 26-46.

Marston, L.C., Bennett, P.C., 2003. Reforging the bond—towards successful canine adoption. Appl Anim Behav Sci 83, 227-245.

Maslow, A.H., 1987. Motivation and personality (3rd ed.). Harper & Row Publishers, New York, USA.

McGreevy, P., Grassi, T.D., Harman, A.M., 2004. A strong correlation exists between the distribution of retinal ganglion cells and nose length in the dog. Brain Behav Evol 63, 13-22.

Mehrkam, L.R., Wynne, C.D.L., 2014. Behavioral differences among breeds of domestic dogs (Canis lupus familiaris): Current status of the science. Appl Anim Behav Sci 155, 12-27.

Melson, G., 2001. Why the wild things are: animals in the lives of children. Harvard University Press, Cambridge, MA.

Meyer, I., Forkman, B., 2014. Dog and owner characteristics affecting the dog-owner relationship. J Vet Behav: Clin Appl Res 9, 143-150.

Millan, C., 2007. Be the pack leader. Three River Press, New York.

Nagasawa, M., Murai, K., Mogi, K., Kikusui, T., 2011. Dogs can discriminate human smiling faces from blank expressions. Anim Cogn 14, 525-533.

Schaan, J., 2011. Dogs as a psychological asset for professionals: a qualitative study of the psychological benefits of human-dog companionship. School of Psychology, Psychiatry and Public Health, Monash University, Victoria, Australia.

Scott, J.P., Fuller, J.L., 1965. Genetics and the social behavior of the dog. University of Chicago Press, Chicago.

Serpell, J., Duffy, D.L., 2014. Dog breeds and their behavior. In: Horowitz, A. (Ed.), Domestic dog cognition and behavior: the scientific study of Canis familiaris. Springer, New York, 31-58.

Shipman, P., 2010. The animal connection and human evolution. Curr Anthrop 51, 519-538.

Thorn, P., Howell, T.J., Brown, C., Bennett, P.C., 2015. The canine cuteness effect: owner-perceived cuteness as a predictor of human–dog relationship quality. Anthrozoös 28, 569-585.

Turati, C., Bulf, H., Simion, F., 2008. Newborns' face recognition over changes in viewpoint. Cogn 106, 1300-1321.

- I8 - UNTANGLING THE NEUROBIOLOGY OF ESCALATED AGGRESSION IN ANIMALS

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Abstract:

Canines' capacity for uncontrolled aggressiveness and violent-like behavior is a serious veterinary medicine concern and inflicts an awful burden on their owners. Unfortunately, the current intervention strategies and treatment options for curbing these problematic behavioral expressions are largely inadequate. Hence, a more fundamental knowledge about the neurobiological determinants of aggression is urgently needed. In particular, the interaction between environmental factors and the neurochemical substrates that causally underlies the shift towards escalated and maladaptive forms of aggressive behavior (e.g., violence) is in great need to be unraveled. Novel experimental laboratory models of violent-like aggression in rodents combined with newly emerging technologies for mapping and manipulating neuronal activity with anatomical, genetic and temporal precision are indispensable to obtain this goal. This contribution presents some of the most significant developments made during the last decade in this understudied preclinical animal research field that promise to significantly advance our understanding of the etiology, brain mechanisms and potential therapeutic interventions of excessive aggressive behaviors.

Keywords: *animal models; aggression; neurobiology; oxytocin; serotonin; vasopressin; violence; 5-HT$_{1A}$ autoreceptors*

Introduction

It is commonly accepted in biology that, throughout the animal kingdom, aggression is one of the most widespread and functional forms of social behavior that ultimately contributes to fitness (procreation) and survival of individuals. Clearly, aggression is the behavioral weapon of choice for essentially all animals and humans to gain and maintain access to desired resources (food, shelter, mates), defend themselves and their offspring from rivals and predators, and establish and secure social status/hierarchical relationships. In both animals and humans, most i ndividuals engage in social conflicts with appropriate and well-controlled (functional) forms of aggressive behavior; only a relatively small percent of individuals may show persistent excessively aggressive behavior or can become extremely violent. This small percentage (ranging from 3-7% in humans and 5-15% in most animals) of escalated aggressive individuals is a major source of death and disability, thus constituting one of the most significant problems for the public health and veterinary medical institutions. Obviously, there is an urgent need to understand these problematic behaviors in terms of their underlying causal mechanisms and modulating factors. In general, animal models are essential to obtain experimental support of the causal nature of physiological and environmental factors in determining particular behavioral expressions. As a matter of fact, a considerable part of our current knowledge on the ethology, etiology, neurobiology, genetics and pharmacology of human aggression is based on experimental and laboratory studies of aggressive behaviors in a wide variety of animals (i.e., ranging from fruit flies, honeybees, ants, crickets, zebra fish, songbirds such as song sparrows and zebra finch, mice, rats, hamsters, prairie voles, dogs, cats and monkeys).
Most neurobehavioral and pharmacological studies of aggressive behavior in the laboratory

setting are performed on rodent species (rats, hamsters, voles and mice) that can show high levels of territorial aggression characteristic of their generally dispersive social structure under low population densities in their natural habitats. Therefore, much of the preclinical aggression research is conducted in territorial male resident rats/mice confronting an intruder conspecific. This so-called resident-intruder paradigm allows the spontaneous and natural expression of both offensive aggression and defensive behavior in laboratory rodents in a semi natural laboratory setting. By recording the frequencies, durations, latencies and temporal and sequential patterns of all the observed behavioral acts and postures in the combatants during these confrontations, a detailed quantitative picture (ethogram) of offensive (resident) and defensive (intruder) aggression is obtained. The resident-intruder paradigm brings this natural form of behavior into the laboratory allowing controlled studies of both the resident aggressor and the intruder victim (Koolhaas et al., 2013). The paradigm is strongly based on the fact that an adult male rat will establish and defend a territory when given sufficient living space, resources and mating partners. Territoriality is significantly enhanced in the presence of females and/or sexual experiences. As a consequence of territoriality, the resident will attack unfamiliar males intruding in its home cage. The intruder in turn will show defensive behavior in response to the offensive attack by the resident. Although typical patterns of aggressive behavior differ between species, there are several concordances in the ethology and neurobiology of aggression among rodents, primates and humans.

Aggressive Behavior: Different Forms in Both Animals and Humans

The existence of different kinds of aggression has long been recognized mainly on the basis of animal research (Blanchard & Blanchard, 1981; Brain, 1979; Adams, 2006). There are generally two types of attacks in both males and females: offensive and defensive. These differ in motor patterns, bite/attack targets, ultimate functional consequences and proximate neurobiological control mechanisms. **Offensive aggression** can be defined as a form of social communication aimed at the (pro)active control of the social environment. The motor patterns for offensive aggression are chase, offensive upright posture, offensive sideways posture, attacks (simple bites or bite and kick), piloerection (bristling) of the fur and teeth-chattering (mainly in rats) or tail-rattling (mostly in mice). In the minutes leading up to intense attack bites, the resident rat emits brief pulses of ultrasonic vocalizations in the 50 kHz ranges that may reflect high excitement The bite targets are primarily the hindquarters of the flanks, back and base of the tail (less-vulnerable body regions). The function is to obtain and retain resources such as space, food, and mates. **Defensive aggression** can be defined as a set of social behaviors performed in defense to an attack by a conspecific or a potential predator. The motor patterns for defensive aggression are flight, defensive upright posture, defensive sideways posture (keep-away), and attacks (lunge and bite). These defensive motor acts are usually accompanied with urination/defecation and emittance of 22 kHz ultrasonic vocalizations. The bite targets are primarily the face (snout), neck, and belly (vulnerable body regions). Defensive aggressive behavior differs from offensive aggression in that bite attacks are not signaled in advance by threats. The function is to defend one's self, mates, and progeny from attacks of another animal of the same or different species. For example, a dominant resident against an unfamiliar male conspecific intruder of the home territory displays offensive behavior (territorial aggression). The offense-defense distinction plays a prominent role in understanding the biology and physiology of animal aggression.
Different forms of aggression are also recognized in humans and the offensive pattern of aggression in animals generally relates to the "hot-tempered" **hostile aggression** subtype in humans (also called **reactive**, **emotional**, **affective**, and **impulsive** aggression). The most basic acts of aggression in humans are: hitting, kicking, biting, pushing, grabbing, pulling, shoving, beating, twisting and choking. Threatening (vocal) and using objects (weapons) to aggress are also included into this definition (Tremblay, 2010). This form of aggression has its strong initiative engagement and autonomic/neuroendocrine arousal in common

with offensive aggression in animals. Moreover, both in animals and humans, this form of aggressive behavior is usually initiated in response to a perceived threat such as the intrusion of an unfamiliar conspecific into the territory or in response to fear and frustration (omission of expected rewards). In contrast, "cold-blooded" **instrumental aggression** (also called **premeditated** and **proactive** aggression) is callous-unemotional aggression that seems to resemble more the quiet-biting attack or predatory forms of aggressive behavior in rodents. Although both male and female rodents perform offensive aggression, there is a clear gender difference in the frequency and intensity of aggression similar to what is generally observed in humans. Males may perform frequent and fierce offensive aggression in a territorial and socio-sexual context. Females show defensive maternal aggression mostly in a maternal context, but low to medium levels of offensive aggression can certainly be observed in all female groups in relation to competition within the social hierarchy (De Jong et al., 2014).
Finally, it should be noted that aggression in both animals and humans has to be conceptualized into two components: trait-like aggressiveness and state-like aggressive behavior. Whereas **trait-like aggressiveness** refers to an individual's predisposition to act persistently aggressive in various different contexts, **state-like aggression** refers to the actual execution of aggressive behaviors. This distinction appears to be of crucial importance when linking certain physiological or neurobiological parameters to aggression.

Development of pathological or deviant forms of resident-intruder aggression

Until approximately a decade ago, most animal studies of aggression were concerned with the ultimate and proximate mechanisms of normal adaptive aggressive behavior, while clinically the focus was predominantly on violent individuals and excessive or inappropriate forms of human aggression. Besides several political, ethical, funding and translational constraints, the lack of biologically relevant and valid animal models for these pathological forms of aggressive behavior is one important reason for the gap in our knowledge about the neurobiological roots and developmental mechanisms of violence in humans. Therefore, new experimental models in preclinical research are being developed that focus more on provoking escalated and uncontrolled forms of aggressive behavior in order to capture the problematic clinical phenotype. Ideally, such models should demonstrate excessive, injurious and impulsive aggressive behavior that exceeds and/or deviates from normal species-typical levels or patterns (see Miczek et al. 2013; de Boer et al., 2009). However, a major obstacle in preclinical animal aggression research is that most laboratory rodent strains are very placid and docile compared to their wild ancestors. In virtually all commercially available laboratory mouse (>500) and rat (>250) strains today, the aggressive behavioral traits, including the putatively underlying molecular genetic components, are dramatically compromised in terms of absolute level and variation. Most likely, this is the result of artificial selection for tame and tractable behavior during the century-long domestication process of this wild-caught animal, being kept, reared and bred in captivity (de Boer et al., 2003)**.** A classic example of this is the maintenance of docile characteristics long after selection for tameness in wild silver foxes even though the behavioral selection criteria are no longer applied, indicating that alleles that predispose to aggression have been removed from the population (Belyaev, 1979)**.**
Consequently, to obtain appreciable levels of offensive aggression in these constitutionally docile laboratory strains, several procedural (often rather artificial) manipulations have been employed to promote and/or enhance the tendency to display offensive aggressive behavior (Table 1 and see de Boer et al., 2009; Natarajan & Caramaschi, 2010 for review).
Obviously, and validly so, some of these procedures have been adopted with the intent to mimic the conditions under which violent behavior in humans occurs (e.g., frustration, maltreatment and stress, instigation, alcohol, drug and anabolic steroid use). Although these experimentally heightened forms of aggressive behavior may to some extent resemble more intense forms when compared to their already low species-typical rates of aggression, they may still fall into the normative range when compared to the patterns and

- **Behavioral/environmental procedures**
  - **Prolonged social isolation (adolescence)**
  - **Maternal neglect/early-life stress**
  - Noxious stimulation
  - Social provocations/instigations
  - Frustrative non-reward experiences
  - **Repeated winning (pleasure)-enhanced**
- **Genetic procedures**
  - **Genetic selection/individual predispositions**
  - Genetic manipulations (targeted deletions, overexpression)
- **Pharmacological/neurobiological procedures**
  - **Brain stimulation/lesion enhanced**
  - **Alcohol-heightened**
  - **Adolescent exposure to cocaine or Androgen Anabolic Steroids (AAS)**

Table 1. Procedural manipulations to induce heightened and/or escalated aggressive behavior.

levels of their wild ancestors. Indeed, higher levels and wider-ranges of spontaneous intraspecific aggression are encountered in feral (wild-derived) or semi-natural populations of rats and mice as compared to their laboratory-bred conspecifics (de Boer and Koolhaas, 2003; Figure 1).

Therefore, an increase in solely the frequency and duration of aggressive acts is only one component of "pathological" aggressive behavior. More productive and relevant animal models of excessive and abnormal forms of aggression should basically demonstrate intense and/or injurious aggression that exceeds normal species-typical levels and patterns. In other words, a form of aggressive behavior that is not subject to inhibitory control anymore and has lost its function in social communication. Hence, this loss of the social communicative nature of the aggressive interaction in the currently available animal models of escalated aggressive behavior are operationally-defined by: (a) Low provocation threshold, short latency to initiate attack; (b) High rate and intensity, leading to significant tissue damage; (c) Disregard of appeasement

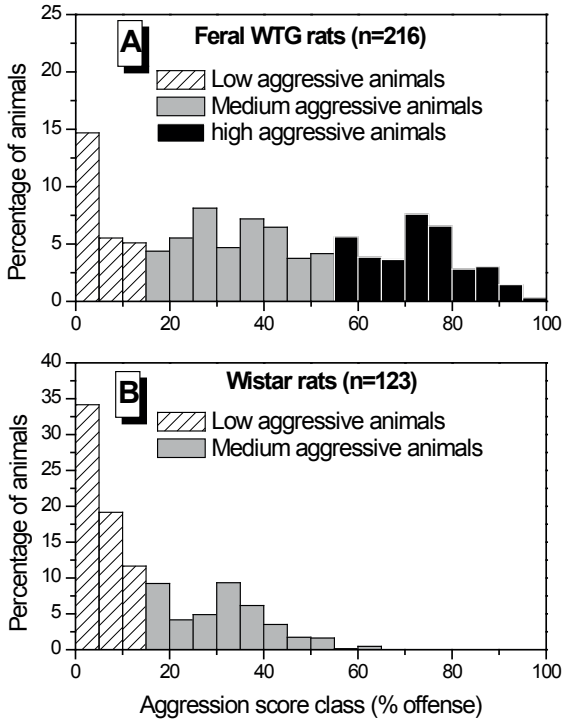

Figure 1. Frequency distribution of offensive resident-intruder aggression in a population of unselected feral Wild-Type Groningen rats (A) and domesticated laboratory Wistar rats (B). Rats are categorized according to their level of aggressive behavior expressed as percentage of time in the RI-test. Note that the highly (> 55 % aggressive behavior) aggressive phenotype is virtually absent in the domesticated rat strain (de Boer et al., 2003).

signals, (d) Lack of species-normative behavioral structure (i.e., attacks are deficient in conveying signaling intention, and lack of context in that critical features of the opponent such as age, sex or situation are misjudged) (Miczek et al., 2013; 2015; Haller & Kruk, 2006; Nelson & Trainor 2007; De Boer et al., 2009). Several of these signs and symptoms of violent-like aggressive display are reliably engendered in the following animal model that has achieved, at least to a variable extent, similarity with human violent aggression in terms of symptomatology and phenomenology (face validity), phylogenetic and ontogenetic origins (construct validity) and response to clinically established treatments using clearly understood neurobiological mechanisms (predictive validity).

Escalated aggressive behavior in unselected feral animals and selective breeding for escalated aggression

Feral or semi-natural populations of rats and mice display much higher levels and a broader range of innate and normal adaptive offensive aggression compared to their highly domesticated laboratory-bred conspecifics (see Figure 1). More interestingly however, clear escalated aggressive and violent characteristics, as defined above, can be engendered in approximately 10-15% of these constitutionally medium to high-aggressive rats that experience repeated victorious episodes of social conflict (i.e., by permitting them to physically dominate other conspecifics for more than 10 times) (see Figure 2). Like humans and other animals, most individual rats respond to these repetitive social conflicts with appropriate and well-controlled functional forms of aggressive behavior, while only a small fraction demonstrate escalated aggression and become violent and destructive. Enhanced levels of offensive aggression and an increased probability of winning an aggressive encounter following previous victories (the so-called "trained fighter" or "winner" effect) was originally already described by Ginsburg and Allee in 1942, and since then has been demonstrated frequently in a wide variety of animal species (see Hsu et al., 2005, for review). Similarly, male wild-derived house mice that were artificially selected for short-attack latencies (i.e., high aggressive SAL mice) show virtually all of the above-mentioned signs of violent aggressive behavior already after 3-5 repeated winning experiences (Natarajan, 2010; Caramaschi et al., 2008).

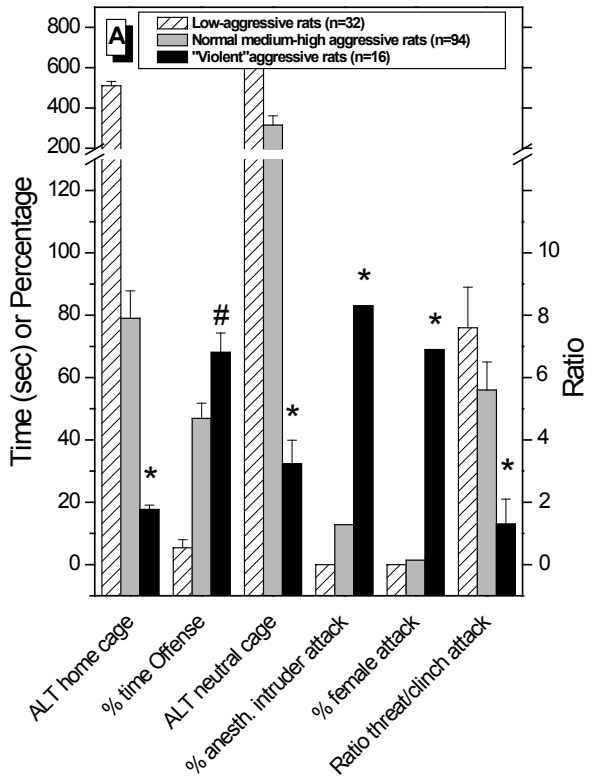

Figure 2. Normal and 'violent' aggressive behavioral characteristics in a small fraction (10-15 %) of resident wild-derived WTG rats before and after multiple (>10) victorious experiences. * indicates significantly ($p<0.05$; student t-test) different from untrained and trained normal aggressive groups.

Thus, upon positive reinforcing or "pleasurable" victorious social experiences, a small group of constitutionally aggressive rats and artificially selected aggressive mice are very prone to show a breakdown of the aggressive behavioral inhibition mechanisms, and transform their initial functional adaptive aggressive behavior into a more violent-like and pathological behavior.

Numerous studies in a wide variety

of animal species have convincingly demonstrated that in addition to securing access to resources, the most intriguing consequence of winning an aggressive conflict is the self-reinforcing or rewarding effect of this type of behavior. Actually, individuals seek out the opportunity to fight and engage in aggressive behavior as a source of pleasure. The most convincing evidence that aggression is rewarding to animals is that the opportunity to engage in aggressive behavior can reinforce operant responding, i.e., animals are willing to work (e.g., bar pressing, nose poking) for aggression as a source of reward and satisfaction (see Miczek et al., 2004 for review). Not surprisingly, just like other positive reinforcers such as food, drugs or sex, the mesocorticolimbic dopamine system is associated with the incentive salience of the rewarding properties of winning fights: Nucleus accumbens (NAcc) dopamine is strongly released during (anticipation of) aggressive episodes (Ferrari et al., 2003) and pharmacological antagonism of dopamine D_1/D_2 receptors in the NAcc diminishes the seeking of the opportunity to fight (Couppis & Kennedy, 2008). In addition, direct optogenetic activation of ventral tegmental area (VTA) dopamine neurons increases aggression (Yu et al., 2014), proving that dopamine function and aggression are causally linked.

This animal model translates well to impulsive aggressive and violent behavior in humans, and in particularly affords the opportunity to identify the plastic neuromolecular changes in the "aggression" control systems that are hypothesized to underlie a shift of normal adaptive aggression into more violent forms (Sluyter et al., 2003; de Boer et al., 2009). For example, in mice that have won territorial disputes repeatedly, a selective enhancement of androgen sensitivity in neural pathways related to motivation (VTS and NAcc) and social aggression (BNST) was observed (Fuxjager et al., 2010). In addition, profound functional changes in the key regulatory sites (5-$HT_{1A/B}$ autoreceptors and reuptake transporters) that control the (re)activity of serotonergic neurons were found to be causally related to the transition into excessive forms of aggression (de Boer et al., 2015).

Neurobiological Correlates of Aggression and Violence

Research of the neurobiology of aggression started with a classic approach of surgical lesioning or electrically stimulating specific brain areas. These experiments were initiated more than 100 years ago with the taming effects of temporal lobectomies in rhesus monkey by Brown and Schafer (1888) and extremely aggressive dogs by Friederich Golz (1890) followed approximately thirty years later by Philip Bard's (1928) demonstration that rage-like aggressive behaviors were absent in posterior hypothalamic knife-cut transectioned cats. Around that same time period, Walter R. Hess started his Nobel Prize-winning intracranial stimulation (ICS) experiments in cats, demonstrating aggressive responses evoked by electrical stimulation of the hypothalamic brain region (Hess, 1943). Since then, neuroscientists have sought to understand the neural basis of aggression and violence by perturbing and monitoring brain activity through a variety of methods and in a wide variety of animals such as monkeys, dogs, cats, rats, mice, voles and hamsters. By employing numerous increasingly sophisticated tools of functional neuroanatomy (i.e., from the classic electric/chemical lesion and stimulation techniques to neurochemical mapping and manipulations), many important strides have been made in understanding the functional brain circuit organization of different social (aggression, sex, parental care) behaviors, i.e., the structurally and functionally highly interconnected "social behavior neural network" (SBN) (Newman, 1999; Nelson & Trainor, 2007).

A Highly Interconnected Network of Brain Regions Controls Aggression

To more comprehensively identify this SBN, and particularly the specific neural circuitry involved in aggressive behaviors, determining the pattern of activation of immediate early gene expression has been employed successfully within the last two decades. Fos is the protein product of an immediate early gene (IEG), *c-fos*, which is expressed in neurons shortly after their depolarization (activation), and then induces expression of downstream genes. Fos-expression can be visualized using immuno-histochemical staining techniques

and the number of Fos-positive neurons in each brain area is used to quantify the activation the area. Application of this technique in offensive aggression paradigms in rats, mice, and hamsters reveals a neuronal network that includes (but is not limited to) the intimately interconnected forebrain (limbic) structures like cortico-medial amygdala (MeA and CoA), bed nucleus of the stria terminalis (BNST), lateral septal area (LS), mediodorsal and anterior thalamus, several hypothalamic nuclei including the anterior hypothalamus (AHA), ventromedial hypothalamus (VMH), lateral hypothalamus (LH), the paraventriculaire nucleus (PVN), the medial prefrontal cortex (mPFC), the midbrain periaqueductal gray (PAG), dorsal raphe nucleus (DRN), locus coeruleus (LC) and ventral tegmental area (VTA) (see Figure 3 and de Boer et al., 2015 for a more detailed review on the neurobiology of offensive aggression). Comparative research indicates that this highly interconnected neuronal network for offensive aggression is remarkably similar in many vertebrate species including humans, indicating that it is evolutionary ancient and very well conserved (Goodson, 2005; O'Connell & Hofmann, 2012). Indeed, this interconnected brain aggression circuitry is generally confirmed in humans by modern brain-imaging techniques such as Functional Magnetic Resonance Imaging (fMRI) and **Positron Emission Tomography** (PET) that allow the *in-vivo* analysis of entire neuronal networks involved in certain types of aggressive behavior. However, it is quite surprising that in most of the human neuroimaging studies, the hypothalamic limbic brain structures involved in the direct control of animal fighting and attack usually do not show up in their region of interest analyses. Rather, these studies predominantly focus on the higher cortical (i.e., prefrontal, cingulate) and temporal lobe (amygdala) brain structures.

The function of the "SBN" brain areas in the expression and control of aggressive behavior ranges from sensory processing and perception up to the generation of somatomotor output patterns, the autonomic and neuroendocrine support of behavior, and all organizational processes in between. However, although the neural circuitry of aggressive social behavior is mapped relatively well in terms of brain (sub)nuclei and its interconnections, it still remains a challenging task to decipher how the activity of distinct sets of neurons within the various nodes of this basic SBN circuitry give rise to different phases (initiation, execution and termination), levels and/or forms of aggressive behavior.

The Hypothalamus as a Critical Brain Region for Offensive Attack

Of all the areas in the brain, the hypothalamus is by far the best-studied region in relation to aggression, ever since seminal lesion experiments found suppression of raging aggressive acts in cats (Bard, 1928) and intracranial stimulation experiments induced this behavior (Hess, 1943). With the development of appropriate stereotaxic instruments, an extensive series of groundbreaking lesion- and electric stimulation studies defined the attack area in the hypothalamus, hence called the hypothalamic attack area (HAA). This HAA consist of an area extending between the LH and the VMH rostrally alongside the anterior hypothalamic nucleus (see Kruk, 2014 for detailed review). Electrical stimulation of parts of the HAA has been reported to induce fierce attack behavior in a variety of animals (e.g., rats, cats, monkeys). This hypothalamically-induced attack behavior can be directed against males, females, anesthetized, or even dead rats, and is directed toward vulnerable body parts. Hence, this form of induced aggression is clearly abnormal and violent-like.

However, despite its anatomical precision, electrodes still affect a rather ill-defined population of neurons and fibers of passage that do not allow definite conclusions on the precise neuronal and circuit-level mechanisms underlying offensive attack. The brain packs roughly 100,000 neurons and a billion synaptic connections in every cubic millimeter of tissue, and electrically stimulating or lesioning even a tiny location in the brain will excite/silence a very large number of intermeshed cells of different kinds. Recently, newly emerging techniques for mapping, measuring, and manipulating neural activity based on genetic targeting of specific neuron subtypes has solved many of these problems. In particular, optogenetics and pharmacogenetics have recently made it possible to rapidly and reversibly activate or

inhibit small molecularly distinct populations of neurons (anatomical and genetic precision) at any moment in time (temporal precision) (Anderson, 2012; Deisseroth, 2014). These revolutionary techniques offer the ability to selectively manipulate individual neural circuit elements that underlie aggression-relevant behaviors. The first experiments investigating the role of the hypothalamus in the regulation of aggression using optogenetic stimulation focused on the ventrolateral subdivision of the VMH. Following virally-delivered expression of the light-sensitive protein channelrhodopsin-2 (ChR2) in this VMHvl region of mice, light pulses delivered through an implanted optic fiber produced robust offensive attacks directed toward male mice, castrated male mice, female mice, and inanimate objects (Lin et al., 2011). Accordingly, inhibiting these neurons using virally-expressed *C elegans* ivermectin-gated chloride channel, which prevents the initiation of action potentials by hyperpolarizing the neurons upon ligand binding (i.e., a pharmacogenetic approach), suppressed normal attacks. Subsequent studies have capitalized on the fact that the neurons of the VMHvl are primarily glutaminergic and are enriched with estrogen receptors of the alpha subtype (Er_{α}). Both Er_{α}-knockout mice and RNAi knockdown of Er_{α} in the VMHvl resulted in a dramatic decrease of natural inter-male aggression (Sano et al., 2013). Most recently, optogenetic stimulation of Er_{α} VMHvl neurons triggered attack behavior whereas optogenetic inhibition suppressed fighting, suggesting that Er_{α} neurons in this small hypothalamic area are necessary and sufficient to initiate and terminate bouts of aggression (Lee et al., 2014). Beside Er_{α}, neurons in the VMHvl also express a variety of other neuromodulator receptors, including serotonin 1A, 2A, 2C, muscarinic acetylcholinergic, and oxytocin receptors. Since many neuromodulators such as serotonin, dopamine and oxytocin change their levels dynamically during the course of aggressive behaviors, they may influence VMHvl neuron excitability and hence aggressive attack. Similar type of opto/pharmacogenetic interrogations and viral vector-based approaches in rodent models of aggression are recently being performed in various other nodes of the brain social aggression circuitry, i.e., amygdala (Hong et al., 2014), prefrontal cortex (Takahashi et al., 2014) and VTA (Yu et al., 2014) and illuminate the precise neuromolecular determinants of aggressive behavior in both its normal and excessive forms.

Neurochemical Modulation of the Aggressive Neural Network

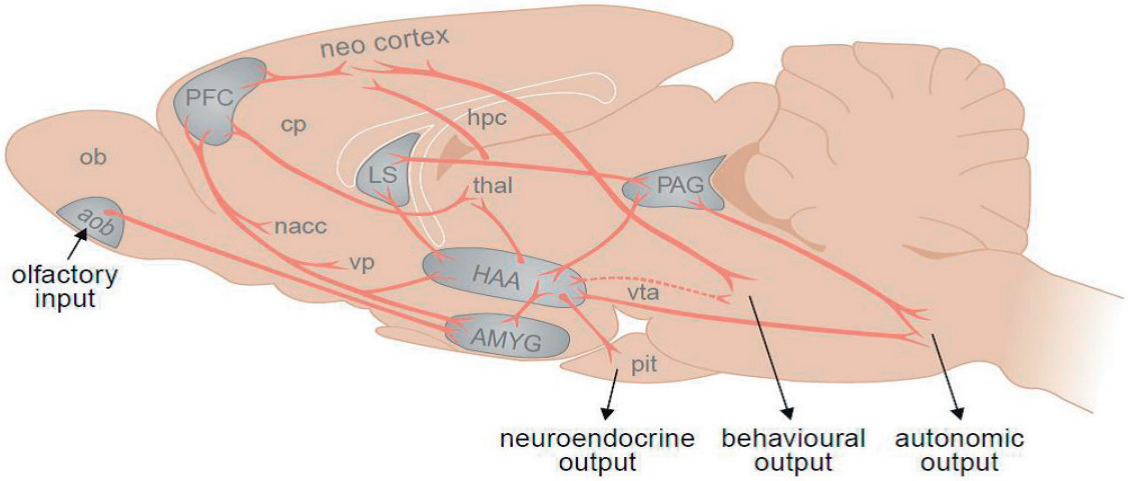

Figure 3. A scheme of the neuronal network in rodents involved in aggressive behavior and the organization of the accompanying neuroendocrine and autonomic activation. (aob=Accessory olfactory bulb; AMYG= amygdala; cp= caudate putamen; hpc = hypothalamus; hpc= hippocampus; LS= lateral septum; nacc= nucleus accumbens; ob= olfactory bulb; PAG= Periaqueductal gray; PFC= Prefrontal cortex; pit= pituitary; thal= thalamus; vp= ventral pallidum; vta= ventral tegmental area).

Obviously, the functional activity of this entire social behavior neural network, and thereby the selection of the appropriate behavioral response to social challenges and opportunities, is determined by a wide variety of molecular substrates (i.e., neurotransmitters, hormones, cytokines, and their respective metabolic enzymes, receptors, and intraneuronal signaling molecules). Undisputedly, among the neurochemical systems that are considered key signaling molecules in this neurocircuitry controlling aggression are the monoamines serotonine (5-HT) and dopamine (DA), the 'social' neuropeptides oxytocin (OXT), and vasopressin (AVP), the 'stress' neuropeptide corticotropin releasing factor (CRF), the 'stress' HPA- and 'sex' HPG-axis's steroid hormones (corticosterone, testosterone, estrogen), and their cognate receptors. Indeed, several studies in wild-type rats and artificially-selected SAL and LAL mice show a widespread central nervous differentiation between the high and low aggressive extremes, for example at the level of the oxytocinergic modulation of the central nucleus of the amygdala (Calcagnoli et al., 2015), the vasopressinergic neurons in the bed nucleus of the stria terminalis and its innervation (density) of the lateral septum (de Boer et al., 2015), the auto-inhibitory control mechanisms of serotonin neurotransmission (see next section). However, the exact functional role of these neurobiological systems in the generation of a particular behavior and/or their behavioral specificity is still far from clear. Moreover, with the notable exception of serotonin signaling components, the causal involvement of these neurobiological substrates in determining aggressive behavior requires further experimental evidence employing the novel opto- and pharmaco-genetic manipulation techniques.

Serotonin is the main molecular orchestrator

All nodes in the neuronal network for offensive aggression are substantially innervated by serotonergic (5-HT) neurons originating in the dorsal and median raphé nuclei in the brain stem (see Figure 4). More than any other neurochemical system, this evolutionary ancient and extremely well conserved neurotransmitter system is generally considered the primary molecular orchestrator of aggressive behavioral traits in virtually every animal species, including man (Siever, 2008; Nelson & Trainor, 2007). However, the direction and exact causal linkage of this association is very complex and it has proven notoriously difficult to unravel the precise role of this amine (and every facet of its synthetic and metabolic pathways, uptake and storage processes, and dynamic receptor signaling mechanisms) in the predisposition for and execution of aggressive behavior in both its normal and pathological forms. For decades, high levels of aggressive behavior are believed to be associated with low brain 5-HT neurotransmission activity. This frequently reiterated serotonin deficiency hypothesis seems consistent with the fact that serotonergic receptor agonists used to mimic higher serotonergic activity, generally reduce aggressive behavior. However, recent studies of the functional status of the 5-HT system before, during, and after the execution of normal adaptive and abnormal pathological forms of aggression have led to a somewhat different view. Display of normal adaptive offensive aggressive behavior aimed at territorial control and social dominance is associated with a higher 5-HT neuronal activity (see de Boer et al., 2015 for relevant references). A negative correlation between aggression and 5-HT as captured in the deficiency hypothesis seems to be a trait-like characteristic of pathological forms of aggression (e.g., violence). For example, a clear positive correlation was found between the level of normal adaptive expressions of offensive aggression and basal cerebrospinal fluid (csf) concentrations of 5-HT and/or its metabolite 5-HIAA. A significant negative correlation between aggression and 5-HT levels was found only upon inclusion of samples from abnormally- and excessively aggressive trained fighter animals. A critical evaluation of the csf 5-HIAA data in aggressive humans confirms this idea that the serotonergic deficiency appears to hold in particular for specific groups of individuals who persistently engage in more aberrant, impulsive and violent forms of aggressive behavior rather than in individuals with instrumental (functional) forms of offensive aggression.

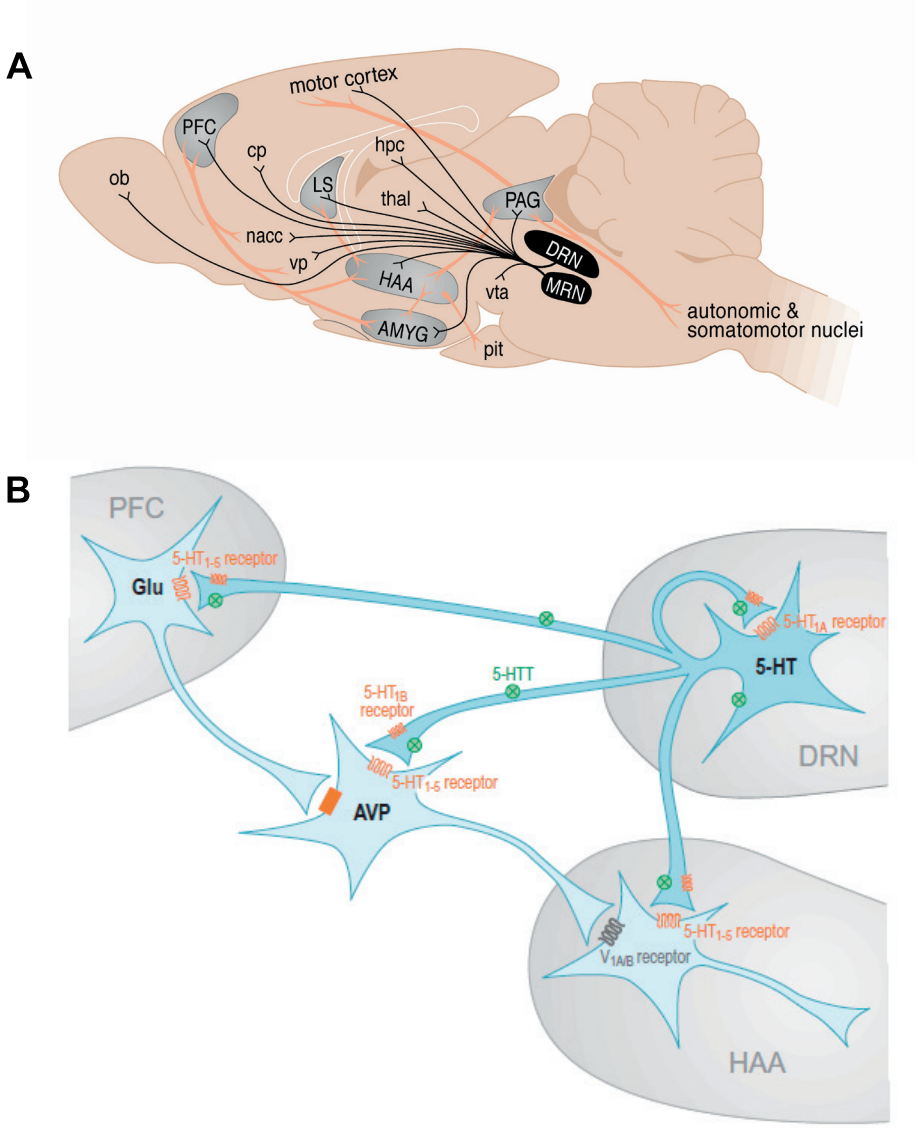

Figure 4.
A) Serotonergic control of the social behavior neuronal network. See legend of figure 3. DRN = dorsal raphé nucleus; MRN = medial raphé nucleus.
B) More detailed neuromolecular characteristics of part of the DRN-prefrontal-HAA microcircuitry involved in the control of aggressive behavior. Glu = glutamate; AVP = arginine vasopressin; 5-HT = serotonin; 5-HTT= serotonin transporter.

Treatment with 5-HT_{1A} or 5-HT_{1B} receptor agonists is one of the most potent pharmacological methods to selectively suppress aggressive behavior in a variety of animal species and experimental paradigms. Apart from acting on receptors at postsynaptic sites, these two receptor agonists also affect the two main serotonergic auto-receptors involved in the negative feedback control of the 5-HT neuron at the level of the synapse (5-HT_{1B}) and at the level of the cell soma (5-HT_{1A}) (see Figure 4). Hence, activation of these receptors by agonists will potently activate the negative feedback and thereby reduce 5-HT firing and neurotransmission. It appears that the potent anti-aggressive effects of these compounds are largely expressed via their action on these inhibitory auto-receptors located at the cell soma and the nerve terminal, by attenuating intruder-activated 5-HT neurotransmission (de Boer et al., 2015).

Interestingly, highly aggressive animals are characterized by upregulated somatodendritic 5-HT_{1A} and terminal 5-HT_{1B} autoreceptor functionality. This considerably (approximately 20-fold) enhanced tonic inhibitory control of serotonergic neurons in aggressive males may explain the negative correlation between baseline levels of 5-HT and escalated aggression found in many species. Furthermore to signify the causality of this correlation, 5-HT_{1A} autoreceptor sensitivity increased or decreased upon enhancing (by repeated victorious experiences) or attenuating (by repeated defeat experiences) aggressiveness, respectively. Notably, animals that escalated their aggressiveness and started to engage in violent-like aggressive behavior demonstrated 5-HT_{1A} autoreceptor super-sensitivity. More persuasively, recent molecular genetic studies have shown that transgenic mice with conditional (at adult age) overexpression of somatodendritic 5-HT_{1A} autoceptors demonstrate suppressed 5-HT neural firing that was associated with a profound hyper aggressive behavioral phenotype (Audero et al., 2013). These data confirm the causal role of tonic 5-HT activity in setting a trait-like threshold for executing overt aggressive behavior.

Vasopressin and Oxytocin as important neuropeptidergic modulators of the social behavior network

Besides their important peripheral physiological functions as neurohypophysial-released hormones, the neuropeptides arginine vasopressin (AVP) and oxytocin (OXT) are also implicated in inter-neuronal communication within various nodes of the social brain network to modulate emotional and social behavioral and physiological responding (Lee et al., 2009a). AVP is generally known to increase anxiety-like behaviors, stress and aggressiveness, whereas OXT has the opposite effects and facilitates social attachment, care, and affiliation (Heinrichs et al., 2009). Existing data from early pioneering work on these neuropeptides convincingly demonstrated opposite roles for AVP and OXT in fear learning processes (Bohus & de Wied, 1998). More recent studies in our wild-type rats and/or artificially selected aggressive (SAL) and non-aggressive (LAL) house mice have demonstrated that high-aggressive animals exhibit higher levels of AVP release when compared to their non-aggressive counterparts (Koolhaas et al., 2010). In addition, there is abundant experimental evidence to support a causal function of vasopressin in proactive aggressive behavior and OXT in passive affiliative behavior. Direct micro-infusion of AVP or OXT into the cerebral ventricles or in selected brain regions facilitates or suppresses, respectively, offensive aggression (Calcagnoli et al., 2015). In addition, a positive correlation between levels of CSF vasopressin and life history of general aggression as well as aggression towards individuals (Lee et al., 2009) has been reported, whereas impaired brain OXT-ergic signaling has been implicated in several human neuropsychiatric disorders associated with social deficits, impulsivity, and excessive aggression (Lee et al., 2009b). Furthermore, mutant mice with the vasopressin receptor V1A/B gene deleted showed virtually no offensive aggressive behavior anymore, whereas elevated aggressiveness was found in mice with deletions of the OXT receptor gene. Consistent with the aggression-promoting of brain AVP, systemic as well as intra-hypothalamic administration of AVP V1A/B receptor antagonists effectively block offensive aggressive behavior in male hamsters and WTG rats (Blanchard et al., 2007; Koolhaas et al., 2009). Basically, an opposite picture seems to emerge for brain OXT signaling. Recent ethopharmacological studies have clearly demonstrated that enhancement of brain OXTergic function, using both intraventricular, intra-amygdalar, and even intranasal administration routes, produced marked anti-aggressive and pro-social affiliative effects that are dose-dependent, behavior- and receptor-selective, and long-lasting (Calcagnoli et al., 2013; 2015).

Based on the findings outlined above, it can be hypothesized that an endogenous balance between vasopressin and oxytocin signaling within (components of) the social behavioral neural circuit may gate the expression of either aggressive or affiliative responses to salient social stimuli.

Synthesis and outlook

A large body of animal neurobehavioral research convincingly demonstrates that abnormal expressions of aggressive behavior principally find its origin in a dysregulation of the deeply rooted neuronal circuits and/or neurochemical pathways in the brain that mediate normal social affiliative-aggressive behaviors. This highly conserved neural and gene expression brain network encompasses neurons in the mesencephalon projecting to hypothalamic nuclei, amygdaloid, septal, prefrontal, and hippocampal forebrain regions, striatal and thalamic loops with the frontal and prefrontal cortex, as well as important feedback loops to limbic and mesencephalic nuclei. The structural and functional properties of this social behavior brain network are established and constantly shaped by a dynamic interplay of genetic and environmental factors (stress, maltreatment, vicarious experiences, substance abuse) in particular during certain sensitive (i.e., perinatal and adolescent) developmental periods. Undisputedly, among the neurochemical systems that are considered key signaling molecules in this neurocircuitry controlling aggression are the canonical monoamines serotonin (5-HT) and dopamine (DA), the 'social' neuropeptides oxytocin (OXT) and vasopressin (AVP), the 'stress' neuropeptide CRF, the 'stress' HPA- and 'sex' HPG-axis's steroid hormones (corticosterone, testosterone, estrogen) and their receptors. Evidently, recent genetic studies in both human and animals have demonstrated that polymorphisms or mutations in a number of genes regulating the functional activity of these important signaling molecules may confer risk factors, either alone but usually in coaction with (early) stressful life conditions, for development of antisocial aggressive traits. Particularly, from the viewpoint of targeting novel molecular sites for intervention, the intrinsic 5-HT autoregulatory mechanisms (i.e., the presynaptic 5-$HT_{1A/B}$ autoreceptors and 5-HTT), and extrinsic neuropeptidergic (i.e., OXT, AVP and CRF) and steroid receptor (i.e., MR and AR) modulatory influences of 5-HT signaling are emerging as important molecular determinants of escalated aggression regulation. Although early efforts during the 1950s and 1960s to translate preclinical neurobiological aggression research findings into clinical use have a sordid history, the current emerging circuit-level knowledge of the neuromolecular underpinnings of escalated aggression has great potential to guide the rational development of effective therapeutic interventions for pathological social and aggressive behavior in both animals and humans.

References

Adams, D.B., 2006. Brain mechanisms of aggressive behavior: An updated review. Neurosci Biobehav Rev 30, 304-318.

Anderson, D.J., 2012. Optogenetics, sex, and violence in the brain: Implications for psychiatry. Biol Psychiatry 71, 1081-1089.

Audero, E., Mlinar, B., Baccini, G., Skachokova, Z.K., Corradetti, R., Gross, C., 2013. Suppression of serotonin neuron firing increases aggression in mice. J Neurosci 33(20), 8678-8688.

Belyaev, D.K., 1979. The Wilhelmine E. Key 1978 invitational lecture. Destabilizing selection as a factor in domestication. J Hered 70, 301-308.

Berkowitz, L., 1993. Aggression: Its causes, consequences and control. Temple University Press, Philadelphia.

Bohus, B., de Wied, D., 1998. The vasopressin deficient Brattleboro rats: a natural knockout model used in the search for CNS effects of vasopressin. Prog Brain Res 119, 555-573.

Brain, P.F., 1979. Differentiating types of attack and defense in rodents. In: Brain, P.F., Benton, D., (Eds.) Multidisciplinary approaches to aggression research, Elsevier, Amsterdam, 53-77.

Brown, S., Schaefer, E.A., 1888. An investigation into the functions of the occipital and temporal lobe of the monkey's brain. Phil Trans R Soc B 179, 303-327.

Calcagnoli, F., de Boer, S.F., Althaus, M., den Boer, J.A., Koolhaas, J.M., 2013. Antiaggressive activity of central oxytocin in male rats. Psychopharmacology 229, 639-651.

Calcagnoli, F., Stubbendorff, C., Meyer, N., de Boer, S.F., Althaus, M., Koolhaas, J.M., 2015.

Oxytocin microinjected into the central amygdaloid nuclei exerts anti-aggressive effects in male rats. Neuropharmacology 90, 74-81.

Caramaschi, D., de Boer, S.F., Vries, H.D., Koolhaas, J.M., 2008. Development of violence in mice through repeated victory along with changes in prefrontal cortex neurochemistry. Behav Brain Res 189, 263–272.

Couppis, M.H., Kennedy, C.H., 2008. The rewarding effect of aggression is reduced by nucleus accumbens dopamine receptor antagonism in mice. Psychopharmacology 197, 449–456.

De Almeida, R.M., Ferrari, P.F., Parmigiani, S., Miczek, K.A., 2005. Escalated aggressive behavior: dopamine, serotonin and GABA. Eur J Pharmacol 526(1-3), 51-64.

De Boer, S.F., van der Vegt, B.J., Koolhaas, J.M., 2003. Individual variation in aggression of feral rodent strains: a standard for the genetics of aggression and violence? Behav Genetics 33(5), 481-497.

De Boer, S.F., Koolhaas, J.M., 2005. 5-HT1A and 5-HT1B receptor agonists and aggression: a pharmacological challenge of the serotonin deficiency hypothesis. Eur J Pharmacol 526(1-3), 125-139.

De Boer, S.F., Caramaschi, D., Natarajan, D., Koolhaas, J.M., 2009. The vicious cycle towards violence: focus on the negative feedback mechanisms of brain serotonin neurotransmission. Front Behav Neurosci 3, 1-6.

De Boer, S.F., Olivier, B., Veening, J., Koolhaas, J.M., 2015. The neurobiology of aggression: revealing a modular view. Physiol Behav 146, 111-127.

Deisseroth, K., 2014. Circuit dynamics of adaptive and maladaptive behavior. Nature 505(7483), 309-317.

De Jong, T.R., Beiderbeck, D.I., Neumann, I.D., 2014. Measuring virgin female aggression in the female intruder test (FIT): effects of oxytocin, estrous cycle, and anxiety. PLOS One 9(3), e91701.

Ferrari, P.F., van Erp, A.M.M., Tornatzky, W., Miczek, K.A., 2003. Accumbal dopamine and serotonin in anticipation of the next aggressive episode in rats. Eur J Neurosci 17, 371–378.

Fuxjager, M.J., Forbes-Lorman, R.M., Coss, D.J., Auger, C.J., Auger, A.P., Marler, C.A., 2010. Winning territorial disputes selectively enhances androgen sensitivity in neural pathways related to motivation and social aggression. Proc Natl Acad Sci U.S.A.107(27), 12393-12398.

Ginsburg, B., Allee, W.C., 1942. Some effects of conditioning on social dominance and subordination in inbred strains of mice Physiol Zool 15, 485-506.

Goltz, F.L., 1884. Ueber die verrichtungen des grosshirns: Funfte abhandlung, Archiv fur die gesammte physiologiedes menschen und thiere 34, 450-505.

Goodson, J.L., 2005. The Vertebrate Social Behavior Network: Evolutionary Themes and Variations. Horm Behav 48, 11-22.

Haller, J., Kruk, M.R., 2006. Normal and abnormal aggression: human disorders and novel laboratory models. Neurosci Biobehav Rev 30(3), 292-303.

Haller, J., Tóth, M., Halasz, J., De Boer, S.F., 2006. Patterns of violent aggression-induced brain c-fos expression in male mice selected for aggressiveness. Physiol Behav 88(1-2), 173-182.

Heinz, A.J., Beck, A., Meyer-Lindenberg, A., Sterzer, P., Heinz, A., 2011. Cognitive and neurobiological mechanisms of alcohol-related aggression. Nat Rev Neurosci 12(7), 400-413.

Heinrichs, M., von Dawans, B., Domes, G., 2009. Oxytocin, vasopressin, and human social behavior Front Neuroendocrinol 30(4), 548–557.

Hong, W., Kim, D.W., Anderson, D.J., 2014. Antagonistic control of social versus repetitive self-grooming behaviors by separable amygdala neuronal subsets. Cell 158, 1348-1361.

Hsu, Y., Earley, R.L., Wolf, L.L., 2005. Modulation of aggressive behavior by fighting experience:mechanisms and contest outcomes. Biol Rev Camb Philos Soc 81, 33-74.

Koolhaas, J.M., de Boer, S.F., Buwalda, B., 2010. Neuroendocrinology of coping styles:

towards understanding the biology of individual variation. Frontiers in Neuroendocrinology 31(3), 307-321.

Koolhaas, J.M., Coppens, C.M., de Boer, S.F., Buwalda, B., Meerlo, P., Timmermans, P.J.A., 2013. The Resident-intruder Paradigm: A Standardized Test for Aggression, Violence and Social Stress. J Vis Exp, 77, e4367.

Kruk, M., 2014. Hypothalamic attack: a wonderful artifact or a useful perspective on escalation and pathology of aggression? A viewpoint. Curr Top Behav Neurosci 17, 143-188.

Lee, H.J., Macbeth, A.H., Pagani, J.H., Young, W.S., 2009a. Oxytocin: the great facilitator of life. Prog Neurobiol 88, 127-151.

Lee, R., Ferris, C., Van de Kar, L.D., Coccaro, E.F., 2009b. Cerebrospinal fluid oxytocin, life history of aggression, and personality disorder. Psychoneuroendocrinology 34, 1567-1573.

Lee, H., Kim, D.W., Remedios, R., Anthony, T.E., Chang, A., Madisen, L., Zeng, H., Anderson, D. J., 2014. Scalable control of mounting and attack by Esr1+ neurons in the ventromedial hypothalamus. Nature 509, 627-632.

Lin, D., Boyle, M.P., Dollar, P., Lee, H., Lein, E.S., Perona, P., Anderson, D.J,. 2011. Functional identification of an aggression locus in the mouse hypothalamus. Nature 470, 221-226.

Miczek, K.A., de Almeida, R.M., Kravitz, E.A., Rissman, E.F., de Boer, S.F., Raine, A., 2007. Neurobiology of escalated aggression and violence. J Neurosci 27(44), 11803-11806.

Miczek, K.A., de Boer, S.F., Haller, J., 2013. Excessive aggression as model of violence: a critical evaluation of current preclinical methods. Psychopharmacology 226, 445-458.

Miczek, K.A., Takahashi, A., Gobrogge, K.L., Hwa, L.S., de Almeida, R.M., 2015a. Escalated Aggression in Animal Models: Shedding New Light on Mesocorticolimbic Circuits. Curr Opin Behav Sci 3, 90-95.

Miczek, K.A., DeBold, J.F., Hwa, L.S., Newman, E.L., de Almeida, R.M., 2015b. Alcohol and violence: neuropeptidergic modulation of monoamine systems. Ann N Y Acad Sci 1349, 96-118.

Natarajan, D., Caramaschi, D., 2010. Animal violence demystified. Front Behav Neurosci 4, 9.

Nelson, R.J., Trainor, B.C., 2007. Neural Mechanisms of Aggression. Nat Rev Neurosci 8, 536-546.

Newman, S.W., 1999. The medial extended amygdala in male reproductive behavior. A node in the mammalian social behavior network. Ann N Y Acad Sci 877, 242-57.

O'Connell, L.A., Hofmann, H.A., 2012. Evolution of a vertebrate social decision-making network. Science 336(6085), 1154-1157.

Raine, A., 1996. Autonomic nervous system factors underlying disinhibited, antisocial, and violent behavior. Biosocial perspectives and treatment implications. Ann N Y Acad Sci S794, 46-59.

Sandi, C., Haller, J., 2015. Stress and the social brain: behavioural effects and neurobiological mechanisms. Nat Rev Neurosci 16(5), 290-304.

Sano, K., Tsuda, M.C., Musatov, S., Sakamoto, T., Ogawa, S., 2013. Differential effects of site-specific knockdown of estrogen receptor alpha in the medial amygdala, medial pre-optic area, and ventromedial nucleus of the hypothalamus on sexual and aggressive behavior of male mice. Eur J Neurosci 37, 1308-1319.

Siever, L.J., 2008. Neurobiology of Aggression and Violence. Am J Psychiatry 165, 429-442.

Sluyter, F., Arseneault, L., Moffitt, T.E., Veenema, A.H., de Boer, S.F., Koolhaas, J.M., 2003. Toward an animal model for antisocial behavior: parallels between mice and humans. Behav Genet 33, 563–574.

Takahashi, A., Quadros, I.M., de Almeida, R.M., Miczek, K.A., 2011. Brain serotonin receptors and transporters: initiation vs. termination of escalated aggression. Psychopharmacology (Berl) 213(2-3), 183-212.

Takahashi, A., Quadros, I.M., de Almeida, R.M., Miczek, K.A., 2012. Behavioral and pharmacogenetics of aggressive behavior. Curr Top Behav Neurosci 12, 73-138.

Takahashi, A., Miczek, K.A., 2014. Neurogenetics of aggressive behavior: studies in rodents.

Curr Top Behav Neurosci 17, 3-44.

Toth, M., Halasz, J., Mikics, E., Barsy, B., Haller, J., 2008. Early social deprivation induces disturbed social communication and violent aggression in adulthood. Behav Neurosci 122, 849–854.

Tremblay, R.E., Szyf, M., 2010. Developmental origins of chronic physical aggression and epigenetics. Epigenomics 2, 495-499.

Tulogdi, A., Toth, M., Halasz, J., Mikics, E., Fuzesi, T., Haller, J., 2010. Brain mechanisms involved in predatory aggression are activated in a laboratory model of violent intra-specific aggression. Eur J Neurosci 32, 1744–1753.

Van Goozen, S.H., Fairchild, G., 2006. Neuroendocrine and neurotransmitter correlates in children with antisocial behavior. Horm Behav 50(4), 647-54.

Veenema, A.H., 2009. Early life stress, the development of aggression and neuroendocrine and neurobiological correlates: what can we learn from animal models? Front Neuroendocrinol. 30(4), 497-518.

Yu, Q., Teixeira, C.M., Mahadevia, D., Huang, Y., Balsam, D., Mann, J.J., Gingrich, J.A., Ansorge, M.S., 2014. Optogenetic stimulation of DAergic VTA neurons increases aggression. Mol Psychiatry 19(6), 688-98.

- I9 - THE SEMIOTIC CANINE: SCENT PROCESSING DOGS AS RESEARCH ASSISTANTS IN BIOMEDICAL AND ENVIRONMENTAL RESEARCH

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Abstract:

The use of dogs in biomedical diagnosis, detection and alert as well as for the search and monitoring of species-at-risk is an emerging field of research. Standard practices are converging towards models that are not necessarily consistent with the well established field of (animal) psychophysics. We briefly discuss the different challenges of applied canine olfactory processing and discuss the adoption of more valid and reliable methods. For mostly historical reasons it seems, scent processing dogs are trained and tested using multiple alternative stimuli in choice tasks (e.g., line-ups including 6 alternative choices, or 6AFC). Data from psychophysics suggest that those methods will reduce or at the very least misrepresent the accuracy of canines. Unless canines are an exception to the rule, sensory, perceptual and cognitive arguments (e.g., Gadbois & Reeve, 2014) can be made against most multiple alternative forced choice tasks (mAFC's) in favor of detection tasks (yes/no and go/no-go procedures) or, as a compromise, simpler discrimination tasks (2AFC or 3AFC at most). We encourage the use of Signal Detection Theory as it focusses on two important factors in defining the validity and reliability of scent processing dogs: 1) It is a robust measure of sensitivity, an important factor in both diagnosis and sensory detection, and, 2) It describes the type of errors (false alarms vs. misses) that a given dog is most likely to commit, allowing for a solid assessment of performance and potentially a readjustment in training. We give an example with Diabetes Alert Dogs (DAD's) specialized in Hypoglycemia Detection in vitro and discuss the potential advantages of keeping a low number of alternatives during training and testing, the importance of low saliency training (LST), as well as adopting pure detection tasks requiring a response commitment from the dogs for both "yes" and "no" responses. The value of d' (a detectability or discriminability measure) and bias measures (criterion) are discussed in the context of canine selection, performance assessment and diagnostic accuracy across applications.

Keywords: *canine olfactory psychophysics; conservation canines; diabetes; hypoglycemia; low saliency training; signal detection theory*

Dogs serve increasingly important roles in a variety of medical assistance and alert positions. Due to their evolutionary close relationship with humans, dogs are very sensitive to behavioral changes and social cues from humans (Miklosi & Topal, 2013). This fact, combined with proper training, results in dogs that can accurately predict seizures (Brown & Strong, 2011), potentially predict migraines (Dawn & Bhowmick, 2013), and serve as anxiety and Post Traumatic Stress Disorder service dogs (Yount et al., 2013). Recently, researchers have become interested in whether dogs can further assist humans by using their noses to diagnose disease and alert to dangerous medical events. It is well known that dogs have incredibly sensitive noses, and empirical studies have revealed dogs detecting cancers with high levels of sensitivity and specificity (Jezierski et al., 2015). Furthermore, the use of diabetic alert dogs to signal hypoglycemic events is becoming more common. Despite a lack of empirical studies examining how dogs detect hypoglycemia, they appear to be benefitting their owners greatly (for reviews see Gadbois & Reeve, 2014; Wells, 2012). Dogs have also been involved in wildlife conservation research to monitor species-at-risk.

The field of canine biomedical detection, diagnosis and alert is expanding rapidly. As teams scramble to develop methodologies, a standardization is still lacking (as discussed by Elliker et al., 2014; Jezierski et al., 2015) despite the likelihood that National Health organizations such as the FDA or Health Canada in North America will require strong Standard Operating Procedures and standardized protocols if canines are to be ever accredited as "diagnostic tools". We believe that the choice of training method will depend on the ultimate goal of the task. Currently, in the literature, the same procedures are commonly used during training conditions, testing conditions (to assess the performance of the dog), and actual diagnostic testing and field deployment. In this paper we identify a few problems in the rationale used with the most popular methods. Let us explore each issue one at a time.

The importance of understanding errors and biases

The stakes are not the same for a mine detection dog (that really cannot afford "misses" or it will pay with its life) and an endangered species search dog (missing a hidden snake during a survey search is unlikely to have dire consequences for the survival of the species or even the local population). Biomedical canines are somewhere in the middle of this spectrum: Detection dogs could be trained to find dangerous bacteria in hospital environments (Bomers et al., 2012), alert to a nocturnal hypoglycemic event with a child that cannot wear a continuous blood glucose monitor (Chen et al., 2000; Wells et al., 2008), or diagnose potential cancers (Jezierski et al., 2015). Those three functions (detect, alert, diagnose) come with different outcomes and corresponding risk assessments, in particular, the cost of making mistakes. The next sections explain what is at stake, how to measure errors and bias, and how to remediate that situation if possible and appropriate.

Not unlike decision theory and diagnostic theory, Signal Detection Theory (SDT) takes into consideration the errors made during judgements. It computes hits (true positives), correct rejections (true negatives) as well as two error types: false alarms (false positives, analogous to type 1 errors in statistics) and misses (false negatives; analogous to type 2 errors in statistics). Most diagnostic toolsets would, from these values, extract sensitivity and specificity scores. SDT goes further: It defines a very robust sensitivity index, d' ("d prime") that can be defined as an index of detectability (in detection tasks) or as an index of discriminability (in a discrimination task). This important distinction calls for a precision: Gadbois & Reeve (2014) distinguish between four psychophysical experimental contexts. We will focus here on the first three, the most likely to be used with scent dog training and assessment. The definitions given below may be slightly oversimplified in the eyes of an animal psychophysicist or sensory neuroscientist, but they cover the essentials of the current trends including one procedural option that we are suggesting. We suggest Kingdom and Prins (2016) or McNicol (2005) for a clear and concise discussion of SDT's parameters. More advanced users of SDT may want to consult Macmillan & Creelman (2005).

We will start with the most cognitive task. Most textbooks (Kingdom & Prins, 2016; Macmillan & Creelman, 2005; McNicol, 2005) discuss identification or recognition tasks. They are typically labelled "matching-to-sample" MTS tasks in the animal literature, and more specifically (implicitly at least) referring to simultaneous MTS (DMTS or delayed matching-to-sample tasks are typically used to specifically study short term memory mechanisms). Technically this task requires the handler to present a sample (standard, sometimes called a "reminder" in cognitive psychology) to the dog (that it will sniff) and then ask the dog to find the match among a number of options, typically 6 in most line-ups, although some will include 8 or 10 choices. Forensic canines (Schoon & Haak, 2009) are the typical example of this approach. As we argued in Gadbois & Reeve (2014), there are issues with this method when the intention is to determine a dog's accuracy. For example, line-ups (6+ choices) add unnecessary perceptual and mnemonic interference (see below for a discussion of interference in multiple choice tasks). In these tasks, every time the dog is asked to match the standard to one of the choices, the standard (sample) may be different. Sample sets can be very small (even just one odor presented as a cursory reminder) or n>2 with no theoretical

limits. Dogs can be presented with 2, 3, 4, … *n* choices of one target and distractors or blanks. A classic line-up of 6 choices is therefore labelled a 6AFC (6-alternative forced choice). If high performance is expected, perceptual and mnemonic interferences are significant beyond 3 choices. This is supported by classical psychophysics (Kingdom & Prins, 2016; Macmillan & Creelman, 2005; McNicol, 2005).

Likely more common is the case of a straight discrimination between multiple options. The animal is expected to identify a target stimulus from a number of distractors (or blanks in early training). Not unlike the scenario above, the dog must choose a target among multiple choices (2AFC, 3AFC, … mAFC). The difference is that typically there is only one odor to identify, and a reminder (i.e., the sample or standard) is not offered (or necessary). This model works well when a basic perceptual discrimination is desired.

The last model, and also the simplest and potentially the most elegant, is a pure detection task. The information processing assumptions are minimal in the sense that the approach identifies a sensory sensitivity (in fact the d' mentioned above). The approach here is to present the dog with one stimulus and requires a "yes" or "no" answer. For that reason, the model is called Y/N and works within the framework of a go/no-go type of response. Note that this model is the most likely to show a bias in the decision pattern from the dog. But what seems at first like a shortcoming should be considered an advantage. A detection task will allow you to most accurately identify your dogs' response biases. If you are planning to use a 2AFC (or other mAFC procedures like line-ups and carousels) the same biases that would be identified in a detection procedure are likely to emerge. In other words, in order to understand the response bias of your dog, the detection task will give you a clearer picture of the response profile and a great context for remediation considering the simplicity of the procedure.

The Y/N model measures bias and quantifies it as a "criterion". There are different criterion measures found in the literature (see Macmillan & Creelman for details) but the basic idea is to categorize a dog along a continuum from a "conservative" to a "liberal" decision maker. Liberal dogs are more likely to give false alarms (and minimize misses) in an attempt to maximize hits. Assuming false alarms are not problematic in the applied context where the dog works (i.e., no negative consequences), this can be a great response profile. It is certainly the one preferred by landmine detection and explosive detection dog handlers. Likewise, a conservative dog will minimize false alarms at the cost of hits, and consequently increase misses.

For now, we will focus on the consequences of knowing this information. Obviously if (and only if) a dog has a bias (and most would, the question would be "how much of a bias" or deviation from what is called in SDT an "ideal observer"), then a trainer can decide if a dog's response profile needs to be modified to change the bias. Modifications can be made by giving feedback on wrong responses, or by changing the reward saliency, frequency, or schedules.

The potential problem with proportion or percentage correct data as performance

Although SDT applies very well to Y/N and go/no-go detection tasks, it can also be applied to 2AFC and mAFC tasks. It is important to realize that some basic assumptions need to be clarified first, namely, if the responding is biased or unbiased. If the responding is unbiased, proportion correct answers are appropriate and can be transformed into a d' (see Kingdom & Prins, 2016 or Macmillan & Creelman, 2005 for computational details). The problem with assuming an unbiased response profile is that it is likely not realistic. If bias occurs, then using proportion correct as a measure of psychophysical accuracy "becomes an invalid measure of sensitivity" (Kingdom & Prins, 2016, page 161). As mentioned above, an even more fundamental issue arises: Although 2AFC tasks are typically easier than Y/N tasks, mAFC tasks tend to be more challenging, with the potential exception of 3AFC tasks (Gadbois & Reeve, 2014; Macmillan & Creelman, 2005; McNicol, 2005). This can be explained fairly easily by pointing out that both sensory-perceptual and mnemonic (working

memory) interference can and will occur as the number of choices presented increases. The mnemonic argument was made in Gadbois & Reeve (2014), but in the case presented there, the working memory load was significant considering that a sample set of 8 stimuli was presented (to be matched to a target in a 6AFC line-up). In most cases when one odor is presented as the sample (or standard), the main interference to worry about is sensory: When dogs sample each odor station in a line-up or carousel, there is a possible sensory interference, not excluding sensory memory especially when the stimuli are of low saliency or if they are very similar (suggesting a low d' value).

Other considerations

We will quickly address a few points before presenting an example based on ongoing research in the Canid Behaviour Research Lab at Dalhousie University. First we would like to point out that SDT is a complex area of psychophysics, sensory psychology and neuroscience and many of the important points could not be expanded upon here (see above for primers and handbook references). The computational aspect of the theory is not very complicated, but requires more space than what is allotted here to cover adequately. One issue that we will mention is the existence of non-parametric models of SDT. Although there are debates about the necessity to apply non-parametric models when they seem to be the most appropriate, some authors argue that the standard SDT theory approximates well enough non-parametric data (see Pastore et al., 2003 for a discussion). Second, the core of the issue lies in the goals of the experimenters, trainers and diagnosticians. Note that when dogs are trained for alert, the most ecologically valid task (including in training) is the detection model. Fundamentally, alert dogs need to signal the presence of the target (e.g., hypoglycemia detection dogs alert to hypoglycemia) and not respond to the absence of the target. This is a typical go/no-go situation and is closer to the Y/N decision task (except that the "no" in the go/no-go task requires no response or the inhibition or a response). In other words, alert dogs do not have an array of stimuli to "compare and contrast". They simply need to alert when the target is present, and inhibit a response when it is not (although, in assessing bias and d', you may want to consider committing the dog to a "yes" response (e.g., nose pointing the target for 5 seconds) and to a "no" response (e.g., sitting back in front the stimulus station). In other cases, it is quite possible that dogs would need to discriminate between similar stimuli that co-occur temporally and spatially. Different strains of a bacteria or parasites to detect may be examples, or as we experienced with our wildlife conservation canines, many occurring species of snakes, with only one being the main target (see Gadbois & Reeve, 2014, for the snake example).

Practical example

In Dalhousie's Canid Behaviour Research Lab, we have developed a training program that allows us to train dogs with no previous sniffer training to detect and discriminate between low saliency odors; specifically, human breath samples. What follows is a brief summary of this training program, and how it was applied in our study aimed at determining whether dogs could detect hypoglycemia in vitro, using breath samples from individuals with Type 1 Diabetes.

An important point to note is that we select our dogs very carefully. We select for dogs that are highly motivated, and that have a very high working drive. As a result, our studies (and most studies of biomedical detection with dogs) test between 3 and 5 dogs. Although this may seem like a small number of dogs with which to complete an empirical study, we are not attempting to provide evidence that *all* dogs are capable of doing biomedical scent detection work, but rather that a few, very carefully selected dogs can be trained to be successful.

The first phase of the training program is Low Saliency Training (LST). Here, we train our dogs to detect Orange Pekoe tea that has been steeped for 5 minutes, and then gradually decrease the saliency of the tea over time by steeping it for less time, and by diluting it with

water. Using a 3AFC procedure (with a reminder), a tea stimulus is presented with two other water stimuli that serve as controls, and the dogs are required to indicate which sample is the tea sample.
If a dog demonstrates the ability to detect the tea stimulus consistently and reliably, the saliency of the tea stimulus is decreased gradually over a series of predetermined saliency levels. Once training with the liquid tea stimuli is completed, we then bridge the gap between tea and breath samples by holding tea in our mouths for 30 seconds, spitting it out, and then breathing through a breath collection tube containing a cotton ball; thus creating a "tea breath" sample. Breath samples are presented against blank cotton ball controls. Once a dog demonstrates the ability to detect the tea breath sample, they are then presented with a clean breath sample. If a dog can detect a clean breath sample successfully, the LST is complete and the dog can now detect human breath.
We find the LST phase important for two reasons: 1. It counters any potential familiarity effects by teaching the dogs to pay attention to stimuli that they have likely ignored most of their lives (human breath), and 2. The LST training serves as an inclusion test by showing us whether a particular dog is capable of detecting low saliency stimuli. If a dog cannot complete the LST successfully, we do not proceed with further training.
After completing the LST we then train the dogs to discriminate between multiple breath samples; first between breath samples from three different individuals, and then between three breath samples donated by one individual at three different times of the day. Again, this phase of training demonstrates to us that a dog is capable of discriminating between competing stimuli and that they are ready to be tested using specific medical samples.
Four volunteer dogs, Nutella, Koda, Bella, and Mist, successfully completed this training program. When we presented the dogs with breath samples donated by individuals with Type 1 Diabetes, we first tested their ability to *discriminate* between three different breath samples obtained from one individual by presenting them with three breath samples simultaneously: One when the blood sugar of the breath donor was hypoglycemic, one when it was normal, and one when it was hyperglycemic, and requiring that the dog identify the hypoglycemic breath sample. We tested their ability to do this with sample sets from three different individuals. All four of the dogs tested were able to discriminate between the samples with average accuracy rates between 90% and 100%.
We then trained Nutella and Koda to *detect* hypoglycemia by presenting them with low, normal, and high samples from one individual sequentially (one sample at a time). Here, the dogs were trained to smell a single sample and indicate whether "yes" this is a hypoglycemic sample, or "no" this is not a hypoglycemic sample. Once they demonstrated the ability to detect the hypoglycemic sample within a sample set, we then added a second sample set (a second hypoglycemic breath sample, a second normal breath sample, and a second hyperglycemic breath sample) from the *same* individual, and tested whether Nutella and Koda could generalize the odor of hypoglycemia to the second sample set; that is, say "yes" to both low breath samples and "no" to all other samples. Presenting the samples in this way allowed us to test whether the dogs could identify multiple instances of hypoglycemia occurring in one individual. As illustrated by the data in Table 1, Nutella was capable of generalizing the odor of low blood sugar to the new breath sample. Koda, however, was not, as illustrated by his low sensitivity score. Although Koda continued to signal "yes" to the first low blood sugar breath sample, he never signaled "yes" to the second low blood sugar breath sample from the same individual.

Table 1. Nutella and Koda's performance on a test of their ability to generalize the odor of hypoglycemia across two breath samples from one individual, using a Go/No-Go procedure.

	Nutella	Koda
d'	1.675	1.468
C	0.313	0.911
Sensitivity	70%	43%
Specificity	88%	95%
Accuracy	78.7%	69%
Precision	84.8%	89%
No. of trials	160	120

As illustrated by the dogs' performance across the two sample presentation methods, presenting the stimuli to the dogs using both 3AFC and Y/N presentation procedures allows for a more thorough understanding of their abilities. Although both Nutella and Koda were able to discriminate between samples successfully (both averaged 100% accuracy), when tested on their ability to detect (Y/N) low blood sugar samples, only Nutella continued to be successful. The "C" in Table 1 represents the criterion (one of the few measures of bias). A positive C indicates a conservative decision maker. The values are from -1 (very liberal) to +1 (very conservative). Both dogs are conservative, but Nutella is the closest to the "Ideal Observer" (meaning that she maximized both correct rejections and hits). Note that Koda has very high specificity. This means that he is accurate at indicating what is *not* a hypoglycemic sample (maximizing correct rejections) but poor at identifying what *is* a hypoglycemic sample (he committed more misses).

Conclusion

When assessing the ability of dogs to diagnose, detect or alert, clear context-appropriate goals need to set before considering a training and assessment protocol. If the goal is to obtain an accurate diagnosis, then procedures resulting in high accuracy (Y/N) and a clear description of the errors and bias need to be adopted (SDT). Even if perfect or close-to-perfect accuracy is not essential, a procedure that can identify error types is still very informative and can influence training or help in selecting "top performance" dogs. Multiple choice procedures such as line-ups increase the sensory and mnemonic interference of the task while reducing performance (percentage correct scores) which may be appropriate during training, but fail to give an accurate profile of the performance of the dog.

References

Blough, D., Blough, P., 1977. Animal psychophysics. In: Honig, W.K., Staddon, J.E.R., (Eds.), Handbook of operant behaviour. Englewood Cliffs, NJ: Prentice-Hall, Inc, 514–539.

Blough, D.S., Lipsitt, L.P., 1971. The discriminative control of behavior. In: Kling, J.W., Riggs, L.A., (Eds.), Experimental Psychology, 3rd ed. NY: Holt, Rinehart and Winston, 743-792.

Brown, S.W., Strong, V., 2011. The use of seizure-alert dogs. Seizure 10, 39-41.

Bomers, M.K., van Agtmael, M.A., Luik, H., van Veen, M.C., Vandenbroucke-Grauls, C.M.J.E., Smulders, Y.M., 2012. Using a dog's superior olfactory sensitivity to identify Clostridium difficile in stools and patients: proof of principle study. The BMJ 345, 1-8.

Chen, M., Daly, M., Williams, N., Williams, S., Williams, C., Williams, G., 2000. Non-invasive detection of hypoglycaemia using a novel, fully biocompatible and patient friendly alarm system. The BMJ 321, 23-30.

Dawn, M.A., Bhowmick, A., 2013. Survey of migraine sufferers with dogs to evaluate for canine

migraine-alerting behaviors. The Journal of Alternative and Complementary Medicine 19, 501-508.

Elliker, K.R., Sommerville, B.A., Broom, D.M., Neal, D.E., Armstrong, S. Williams, H.C., 2014. Key considerations for the experimental training and evaluation of cancer odour detection dogs: lessons learnt from a double-blind, controlled trial of prostate cancer detection. BMC Urology 14, 1-9.

Engen, T., 1971. Psychophysics 1: Discrimination and detection 11-46.

Gadbois, S., Reeve, C., 2014. Canine olfaction: Scent, sign, and situation. In: Horowitz, A. (Ed.), Domestic dog cognition and behavior. Springer, New York, 3-29.

Jezierski, T., Walczak, M., Ligor, T., Rudnicka, J., Buszewski., 2015. Study of the art: Canine olfaction used for cancer detection on the basis of breath odour. Perspectives and limitations. Journal of Breath Research 9, 1-12.

Kingdom, F.A.A., Prins, N., 2016. Psychophysics. A practical introduction. Elsevier.

Macmillan, N.A., Creelman, C.D., 2005. Detection theory. A user's guide (2nd ed.). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

McNicol, D., 2005. A primer of signal detection theory. Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

Miklósii, A., Topàl, J., 2013. What does it take to become 'best friends'? Evolutionary changes in canine social competence. Trends in Cognitive Sciences 17, 287-294.

Pastore, R.E., Crawley, E.J., Berens, M.S., Skelley, M.A., 2003. "Nonparametric" A' and other modern misconceptions about signal detection theory. Psychon Bull Rev 10, 556-569.

Schoon, G.A., Haak, R., 2002. K9 suspect discrimination: Training and practicing scent identification line-ups. Calgary, Alberta: Detselig Enterprises.

Wells, D., 2012. Dogs as a diagnostic tool for ill health in humans. Alternative Therapies in Health and Medicine 18, 12-17.

Wells, D., Lawson, S.W., Siriwardena, N., 2008. Canine responses to hypoglycemia in patients with Type 1 Diabetes. The Journal of Alternative and Complementary Medicine 14, 1235-1241.

Yount, R., Ritchie, E.C., St. Laurent, M., Chumley, P., Olmert, M.D., 2013. The role of service dog training in the treatment of combat-related PTSD. Psychiatric Annals 43, 292-295.

- I10 - THE EFFECT OF OXYTOCIN ON HUMAN-DIRECTED SOCIAL BEHAVIOUR IN DOGS *(Canis familiaris)*

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Abstract:

The oxytocin system has recently received increasing attention due to its effect on complex human behaviours. In parallel to this, over the past couple of decades, the human-analogue social behaviour of dogs has been intensively studied. Combining these two lines of research (e.g. studying the relationship between dog social behaviour and the oxytocin system) is a promising new research area. The present paper will review the existing literature on how oxytocin is related to different aspects of human-directed social behaviour in dogs.

Keywords: *dog; oxytocin; social behaviour*

Oxytocin – which undoubtedly plays a central role in the expression of the high levels of sociality that are essential to contemporary human behaviour (Carter, 2014) – is in evolutionary terms a remarkably conservative nonapeptide, that plays a particularly prominent role in the modulation of social life across mammalian taxa (Yamasue et al., 2012). However, although there is a general agreement on the prosocial effects of oxytocin, there are various arguments about how these are mediated and the differences between viewpoints are often implicit rather than clearly delineated (Campbell, 2010). Much of the debate focuses on methodological issues about which are the low level (e.g. cellular) mechanisms behind the oxytocin effects and how results of different studies can be compared (Quintana et al., 2014). Our current knowledge of the behavioural effects of oxytocin in humans is mainly based on three mostly independent approaches: (i) correlational studies measuring oxytocin in the periphery (urine, saliva, blood) or in the Cerebro-Spinal Fluid, (ii) gene × behaviour association studies involving receptor (OXTR) polymorphisms, and (iii) experimental studies manipulating (both the peripheral and central) levels of oxytocin using intravenous or intranasal administration (for an evaluation of these approaches regarding their informative value in terms of the underlying central nervous mechanisms see: Heinrichs et al., 2009).
The number of published papers on dogs (social) cognition is rapidly growing (Bensky et al., 2013) due to the fact that dogs have been proven to display human-analogue social skills (Hare & Tomasello, 2005; Miklósi & Topál, 2013). Thus not surprisingly investigations of the relationship between the oxytocin system and dog social behaviour have also begun.

The effect of dog–human social interaction on peripheral oxytocin levels

The first studies aiming to unravel the relationship between oxytocin and human-directed social behaviour in dogs tested the effect of positive social interaction on peripheral oxytocin levels. It was found (Odendaal, 1999; Odendaal, 2000; Odendaal & Meintjes, 2003 – data of same subjects published with slighly different focus) that dog – human social interaction increases both dogs' and humans' blood oxytocin level (as measured by high-performance liquid chromatography technique – HPLC) compared to baseline (before interaction). Other physiological changes included increased levels of beta-endorphin, prolactin, phenylacetic acid and dopamine, as well as decreased heart rate. The social interaction in these studies consisted of a maximum 30 minutes session (the intervention was finished when a stable drop of at least 5-10 % in blood pressure was experienced) including softly talking to the dog, gently stroking the dog with long smooth strokes, low-key playing and scratching the

body and ears of the dog. Participants (N=18) were both owners with their private dogs and non-owners with dogs from the animal facility of the University of Pretoria. These results were conceptually replicated (Handlin et al., 2011) on N=10 female volunteers and their own male Labrador dogs. At the end of a 3-minute-long interaction, which consisted of petting and stroking different parts of the dog's body and talking to it, an increase in blood oxytocin level was found (using immunoassay technique). Stroking the abdominal area for 15 minutes without social reinforcement such as vocal encouragement and eye contact by experimenters who knew the dogs well, but were neither their owners nor caregivers was also found to increase peripheral oxytocin levels as measured (using radioimmunoassay technique) from urine samples 1 hour after the initiation of stimulus (Mitsui et al., 2011). In this experiment (N=9) dogs from different breeds were tested and stroking was found to increase oxytocin levels compared to baseline similarly to other reinforcing treatments such as eating and exercising, but not drinking water. Reunion with a familiar person was also found to increase blood oxytocin levels in (N=12) laboratory-kept beagle dogs (measured with immunoassay) compared to a pre-separation baseline phase (Rehn et al., 2014). Furthermore if the familiar person made both physical and verbal contact with the dogs upon reunion oxytocin levels remained higher than baseline in the post-reunion phase as well (but not with verbal contact only or when ignoring the dog). These results (and others not measuring dog oxytocin levels directly) have led to the supposition that the oxytocin system plays a crucial role in dog–human interactions and serves as a potential underlying mechanism behind animal assisted therapy (Beetz et al., 2012; Romanciuc et al., 2014).
In a questionnaire-based study (Handlin et al., 2012) blood samples were collected from N=10 male Labrador dogs' (same subjects as in Handlin et al., 2011) and measured mean oxytocin levels (immunoassay) during a 60-minute period including a 3-minute social contact with the owner at the beginning. It was found that dogs' mean oxytocin levels were related to items indicating the intensity of the dog–owner relationship (as measured by the Monash Dog Owner Relationship Scale). There was a positive correlation with the frequency of owners kissing their dogs and the perceived bond with the dog, and a negative correlation with the frequency of giving food treats to their dog. Higher oxytocin levels in the dogs were also associated with the owners having a perception of their dogs being less difficult to look after and less thought of as making a mess. These results can be due to both differences in baseline oxytocin levels as a function of the above psychological characteristics as well as a differential reaction to social interaction with the owner depending on their relationship. It has also been found (Kanizsár et al., 2012) that a 10-minute-long social interaction (eye-contact, petting) with the owner has behavioural effects consistent with endogenous oxytocin increase. Dogs' (N=60) social susceptibility increased after pre-exposure to social stimuli so that in a food choice task subjects were more likely to change their own preferences for the large quantity of food and tended to follow the human demonstrator's choice in comparison with dogs pre-exposed to non-social pre-treatment (solitary play with a dog toy).
A more recent study (Romero et al., 2014) found that in an experimental situation where owners of the dogs were instructed to sit quietly and not to actively interact with their dogs, neither the time subjects spent in close proximity to their owners nor the affiliation subjects provided to or interchanged with them was related to the oxytocin increase ratio (post-test / pre-test OXT levels). In a similar experimental situation (Nagasawa et al., 2015), where the owner was instructed to remain seated in a chair, but was otherwise free to interact with his/her dog during 30 minutes, it was found that dogs (N=8) that gazed longer to their owner showed a higher oxytocin change ratio (as measured from urine samples collected right before and 30 minutes after the interaction) compared to dogs (N=22) that gazed shorter to their owner. The duration of dog-to-owner gaze significantly explained the oxytocin change ratio in dogs and the oxytocin change ratio in owners correlated significantly with that of dogs. Furthermore in case of hand-raised wolves (N=11), who did not gaze at their 'owners' (animal management professionals) and thus gazed significantly less than even dogs in the short gaze group the duration of wolf-to-owner gaze did not correlate with the

oxytocin change ratio in either owners or wolves. These results have prompted the authors and others (Maclean and Hare 2015) to speculate about an oxytocin-gaze positive loop and the coevolution of human-dog bonds. Others (Fiset & Plourde, 2015), however, have suggested that any conclusions about the coevolutionary process are premature and should be presented with great care. It has been argued for example that the oxytocin feedback loop (present in mother–infant relationships, possibly also in case of dog pups and their mothers) may have simply been generalized to various behaviours and to any dog's primary caregiver, whether they are human or not. It has also been suggested (Kekecs et al., 2016) that some confounding factors in the experimental design and data analysis prevent us from concluding that an oxytocin-gaze positive loop was acquired during dog domestication even if the importance and originality of this study is undeniable. Specifically the authors of this commentary argue that there are several confounding differences between the dog and wolf arm of the experiment such as owner sex (82% female for dogs and 55% female for wolves) and re-analysis of the original data shows that oxytocin increase is evident in women owners of both dogs and wolves while oxytocin did not change or even showed a slight decrease in men. Furthermore there was a significant difference in the baseline oxytocin values of the dog and wolf owners (thus the apparent difference between dogs and wolves may be simply due to a ceiling effect), and the rearing and socialization of animals was also different. It is also claimed that the statistical methods applied for hypothesis testing are inappropriate, and while the group-by-group analyses showed different data patterns for dogs and wolves, re-analysing the original dataset building one statistical model yielded no significant group-predictor interaction effects. A further confound relates to statistical power: correlation between animal-to-owner gaze and oxytocin change is based on a sample of N=28 dogs and N=11 wolves and it can be demonstrated with bootstrap sampling from the dog dataset that even if the correlation between gazing and oxytocin change was as high in the wolf population as that found in the dog group, a sample of 11 wolves would not reveal statistically significant correlation in 71% of the samples. As a solution to this problem (and taking into account the scarcity of wolves available for such experiments) it has been suggested to take several samples from the same animal (and owner) at different time-points or at different experimental sessions thus taking into account inter-individual correlation using mixed models.

Associations between the polymorphisms in oxytocin receptor gene and social behavior

Another line of research has focused on genetic polymorphisms related to the key component of the oxytocin system, the oxytocin receptor gene (OXTR) and its association with dog behaviour. It had already been shown that the similarity between the human and the dog OXTR gene is high (Marx et al., 2011), although a 5-aminoacid-long sequence is missing from the dog OXTR that is present in humans and the *in silico* addition of this sequence to the dog OXTR results in a considerable protein structure change. The dog OXTR protein is 384 amino acid long (compared to the 389 amino acid long human protein) and compared to the human protein contains different amino acids at 26 locations (out of these 8 amino acids have similar chemical properties such as polarity, acidity). Single nucleotide polymorphisms (SNPs) were identified by direct sequencing of the protein coding segment and the flanking regulatory un-translated regions in both different dog breeds and wolves on N=3 individuals per group (Bence et al., 2013). Five novel (-213AG, -93TC, -73CG, -49CG, 19131AG) and three known (rs22927829, rs8679682, rs8679684) SNPs were found and genotyped in larger populations involving German Shepherds (N=71), Border Collies (N=104), Labrador- and Golden Retrievers (N=64), Beagles (N=29) and wolves (N=44). The results confirmed that the identified SNPs are polymorphic not only in the dog breeds, but also in wolves, however allele frequencies differed among the investigated breeds as well as between dogs and wolves.

Kis et al. (2014a) was the first to use the candidate gene approach in dog oxytocin research. Behaviour in every-day social situations was assessed in association with SNPs in the

regulatory regions (5′ and 3′ UTR) of the OXTR (polymorphisms: rs8679684, −213AG, 19131AG) in German Shepherds from Hungary (N=104) and in Border Collies from Hungary and Belgium (N=103). Results show that these SNPs have an impact in both breeds on proximity seeking, and on friendliness towards strangers, although in the latter case an opposite trend was found for the two breeds. A further study (Kubinyi et al., submitted) also found that two of these polymorphisms (19131AG, rs8679682) were related to greeting behaviour of racing Siberian Huskies (N=96). Both allele frequencies and the direction of the observed gene × behaviour associations were strikingly similar to those found in Border Collies: Siberian Huskies with the GG genotype approached an unfamiliar person in a non-aggressive way more frequently in the greeting test and Border Collies with GG genotypes achieved higher scores on a friendliness scale. Note, however, that in case of the Border Collie study (Kis et al., 2014a) the friendliness scale was composed of the dogs' behaviour in reaction to a threatening stranger and to a passive stranger when facing a problem situation, while the greeting test was part of the proximity seeking scale that was not associated with 19131AG, but with -213AG (not tested in the Siberian Husky study due to Hardy-Weinberg disequilibrium). The association between the OXTR and human-directed social behaviours was conceptually replicated on sample of Border Collies from Austria (N=170) using similar everyday social situations (Turcsán et al., 2014). Confirming previous results associations with dogs' proximity seeking and friendliness were found. Furthermore a previously not investigated polymorphism in the second exon (rs8679682) was associated with dogs' separation behaviour, their tendency to look at humans in problem situations, their obedience to simple commands and their reaction to a threatening stranger. It was also found on a sample of Border Collies that reaction to ambiguous social stimuli is related to polymorphisms in the OXTR gene (Park et al., 2014). Eighteen behavioural variables were recorded in 7 tests on N=86−98 dogs (varying across tests) and the following behavioural variables were associated with OXTR SNPs (rs8679682, -94TC and -74CG): frequency of looking at a helper after seeing a motionless person on all four, latency of breaking eye-contact with a neutral person, number of correct choices following a non-communicative gaze cue, and latency of approaching the non-indicated food location. Importantly a difference in gene × behaviour association patterns was found between the Border Collie populations of the two countries (Austria and Hungary) involved in the study.

A more recent study (van Rooy et al., 2016) investigated the OXTR gene as a candidate in Golden Retrievers with separation anxiety. The potential relationship between the oxytocin system and canine separation anxiety was originally proposed in a review article by Thielke and Udell (2015), although the authors of this publication made their suggestion in the context of treating separation anxiety with intranasal oxytocin administration. Van Rooy and colleagues (2016) have investigated in a case−control design (N=42 dogs: 24 affected by separation anxiety based on an owner-report questionnaire and 18 non-affected controls) if separation anxiety is associated with 45 SNPs within 500 kilobases of OXTR (Illumina HD 170,000 SNP array), but they found no such evidence. One OXTR haplotype (CCA, SNP 9503004) had a raw p-value of association less than 0.05 with a 0.72 versus 0.50 frequency for case and control respectively, but this p-value did not remain significant after permutation. There is, however, evidence that an OXTR SNP (-213AG) is related to Border Collie dogs' (N=135) attachment towards their owners as measured in a Strange Situation Test (Kovács et al., in prep). Another study (Oliva et al., 2016b) has looked at microsatellites at various distances from the OXTR gene in buccal samples of N=75 pet- and blood samples of N=94 shelter dogs of various breeds and mixed breeds as well as in buccal samples of N=12 human-reared wolves (mix of the subspecies: Arctos, Occidetalis and/or Nubilus). Results showed that out of the eight primers investigated the two closest to the OXTR gene (located at 9.36 million base pairs within the genome), located at 9.11 million and 9.66 million base pairs respectively were significantly associated with species (dog versus wolf). The authors have also looked at the performance of their pet dog subjects in an object choice task with 20 trials of momentary distal pointing after both oxytocin and placebo pre-treatment.

There was no significant association between performance (good performers that scored ≥ 18/20 versus poor performers that scored ≤ 12/20) and any of the primers. There was also no significant association between oxytocin response (high oxytocin responders that improved their performance by 3-7 points between sessions versus poor responders whose performance remained the same or declined between sessions) and any of the primers.

The effect of exogenous oxytocin administration on dogs' social behavior

The third approach, experimental manipulation of oxytocin levels, has also been used in dogs. Intravenous administration was validated (Mitsui et al., 2011) by measuring oxytocin (OXT) levels in both blood and urine samples following the injection of 4 times 0.25 ml OXT during the course of 15 minutes. Plasma OXT concentration reached a maximum immediately after the fourth injection (15 minutes after baseline) and then rapidly returned to baseline levels. The peak urinary OXT concentration occurred 1 hour after baseline (45 minutes after the fourth injection) and returned to baseline levels slowly (by the end of the 2nd hour after baseline). A more widely used alternative to study the effect of oxytocin on behaviour is intranasal (instead of intravenous) oxytocin administration (IN-OXT). It was found (Romero et al., 2014) that 15 minutes after administering 40 IU oxytocin intra-nasally blood OXT levels were elevated compared to both baseline and placebo condition in N=5 dogs. (OXT concentrations were also higher 90 minutes after OXT administration compared to placebo condition, but the difference did not reach statistical significance – p=.080.) Urinary oxytocin concentration of the same subjects was also higher 90 minutes after OXT administration (compared to both baseline and placebo condition) and the increase in urinary OXT levels correlated with the accumulate value of plasma OXT. Heart-rate variability was measured in the same study during the 5-minute intervals before and after the IN-OXT administration and it was found that high frequency (HF; computed by spectral analysis for NN intervals in the range of 0.15 – 1.00 Hz) decreased right after spray administration independent of treatment received, and during the subsequent 5 minutes it did not significantly vary in the placebo group, while it showed a significant increase in the oxytocin group. Another study (Kis et al., 2014b) found similar results on N=10 pet dogs by showing in a within-subject design that 40 minutes after intranasal administration of 12 IU oxytocin heart rate (HR) decreased and heart rate variability (HRV; standard deviation of RR intervals) increased compared to the placebo group (as measured during a 1-minute-long interval). The same measurement was repeated (Kovács et al., 2016) on N=39 dogs and apart from confirming that 12 IU oxytocin decreased HR and increased HRV 40 minutes after IN-OXT treatment, it was also found that changes in HR and HRV were related to behaviour in the subsequent experiment (biological motion perception task, see later).

The first study to assess the effect of IN-OXT treatment on dog behaviour (Romero et al., 2014) measured affiliative behaviour during a 60-minute period immediately following the administration of 40 IU oxytocin. The owners of the dogs were instructed to sit quietly in an experimental room and not to actively interact with their dogs, thus any behaviour directed from the dogs to their owners was either ignored or only briefly reciprocated (e.g., dogs received a gentle brief touch or push back when they tried to lick their owner's face). Dogs administered with OXT initiated affiliation (defined as sniffing, licking, gentle touching with the nose or paw, play bouts, and body contact excluding tails) toward their owners more often compared to placebo treatment. Furthermore following OXT administration dogs showed an increased social orientation to their owners (defined as staring, looking at owner or no clear gaze direction but head frontally oriented to owner). Effects of IN-OXT treatment on social behaviour towards conspecifics were also documented in this study as well as in a follow-up analysis (Romero et al., 2015). Other studies have focused on the applied aspects of IN-OXT research. It was found (Kis et al., 2015) that dogs (N=64) that received 12 IU IN-OXT showed an increased positive expectation bias in the cognitive bias paradigm 40 minutes post treatment compared to placebo groups, and this effect was more pronounced in a communicative compared to a non-communicative context. Moreover in a

threatening approach test (N=36) IN-OXT pretreated dogs (12 IU) looked back more at the experimenter standing behind them (40 minutes post treatment), that can be interpreted as social referencing in a mildly stressful situation (Hernádi et al., 2015).
The canine analogues of human communicative skills were also investigated. It was found (Oliva et al., 2015) that the administration of 24 IU IN-OXT enhanced the appropriate use of human (momentary distal) pointing and gazing 45 minutes post treatment in dogs (N=62) in a two-way choice task where subjects had to locate hidden food based on human social cues. A further interesting finding of this study is that dogs' enhanced pointing-following performance was maintained for the second test session 5-15 days after IN-OXT administration, that is dogs that received the placebo treatment for the second session (after having received IN-OXT for the first session) performed better compared to dogs that received placebo treatment during the first session; no order effect (first vs. second session) was found for the oxytocin treated dogs. A follow-up analysis (Oliva et al., 2016a) has further shown that while dogs' ability to follow both human pointing and gazing is predicted by owner reported questionnaire measures (anxious attachment in owners, and contagion of human emotions respectively), no such correlation can be found for their performance following IN-OXT treatment. The finding that dogs' performance in following human momentary distal pointing is enhanced by IN-OXT treatment was conceptually replicated with a slightly different methodology (Macchitella et al., in prep). Subjects (N=14, including puppies as young as 4-month-old) received 2 IU/kg IN-OXT (with their weight ranging from 5 kg to 40 kg) or placebo in a within subject design (with 1–22 days between sessions) and participated in a pointing following task at their homes or at a veterinary centre 15 minutes post treatment. While their results confirmed that dogs chose the baited cup significantly more often in the oxytocin compared to the placebo condition (with dogs in the placebo condition also performing above chance), no effect of subjects' age, test location or order of treatment was found (although the relatively low sample size might not allow for such comparisons). Also, gazing behaviour in female (N=15; 2 gonadally intact, 13 spayed) but not male (N=15; 2 gonadally intact, 13 castrated) dogs was found to increase during a 60-minute period immediately after IN-OXT (40 IU) treatment (Nagasawa et al., 2015). In this experimental situation the owner and two unfamiliar people were seated in a room and human behaviour toward dogs was restricted (they were forbidden to talk to each other or to touch the dog voluntarily). These results, together with the finding that no significant oxytocin change ratio was found in dogs when interaction with humans was limited, is interpreted as further evidence for an oxytocin-gaze positive feedback loop (see above) although no explanation exists for the sex differences found in this but not their previous study.
Another experiment (Tóth et al., in prep) has found that after presenting subjects (N=39) with yawns or mouth openings, contagious yawning was observable in the IN-OXT (12 IU, 40 minutes post treatment), but not in the placebo group. However, as the number of yawns correlated with other signs of stress/anxiety but did not correlate with questionnaire-measured empathy, this result is probably due to the decreased social stress after IN-OXT, and not changes in empathy. In a food preference (small versus big quantity) task IN-OXT enhanced dogs' (N=37) susceptibility to the experimenter's counterproductive preference (Kis et al., in prep). Using an eye-tracking paradigm it was found in a within-subject design that 40 IU IN-OXT increased the number of fixations laboratory-kept beagle dogs (N=42) made at the eyes of smiling human faces, and it diminished dogs' tendency to revisit the eyes of angry faces more often 45 minutes post treatment (Somppi et al., 2016). A parallel eye-tracking study (Hernádi et al., in prep) also found that IN-OXT (8 IU for dogs under 18 kg of weight and 12 IU for dogs over 18 kg) has and effect on (N=38) pet dogs' viewing patterns of (male) human emotional faces 35-45 minutes post treatment. However, the results of this study are slightly different as it was found that oxytocin decreases dogs' preferential looking to the eye region of human faces regardless of the displayed emotional expression. The effect of IN-OXT (12 IU) on basic mechanisms of social cognition was also investigated using the biological motion paradigm (Kovács et al., 2016). Dogs (N=39; 40

minutes post treatment) were presented with a moving human point-light figure and its inverted and scrambled version. Results showed that while placebo-pretreated dogs showed a spontaneous preference for the biological motion pattern as expected, there was no such preference after IN-OXT.

While the above studies have predominantly used a mixed sample of several dog breeds and crosses or alternatively focused on one single breed, a recent study (Kovács et al., in prep) provides evidence that IN-OXT treatment has differential effects on different dog breeds. Border Collies (N=19) and Siberian Huskies (N=19) were tested in situations measuring social responsiveness, and apart from pretreatment (OXT/PL) and breed effects interactions among these two factors were also found in case of several behavioural variables. For example Border Collies, but not Siberian Huskies, looked more at the experimenter after oxytocin administration in the 'Unreachable food' situation; and oxytocin-pretreated Border Collies looked longer at the experimenter's eyes compared to oxytocin-pretreated Siberian Huskies in the 'Tolerance of prolonged eye contact' test, while there was no difference between the two breeds after placebo treatment. These results are not surprising as due to the differential selection of the two breeds (cooperative versus independent workers) they are genetically distinct, and as they are kept for different purposes and thus have different experiences epigenetical changes in the oxytocin system might occur during ontogeny.

Conclusions and future directions

The above outlined studies all point to the direction that oxytocin plays a complex role in regulating human–dog relationships. This is evidenced by the impact of genetic polymorphisms in the oxytocin system (OXTR gene), and exogenous oxytocin on different aspect of social behaviour towards humans, as well as by the finding that behavioural treatment with human social stimuli influence oxytocin levels. However, several methodological discrepancies exist between the published studies (especially in case of the IN-OXT research), due to the fact that different research groups started to simultaneously and independently work on this topic, that might make future work and comparison of results difficult. There is no way to tell which method is better, but a consensus should be reached in the following points: i) dose and delivery method of IN-OXT treatment, ii) duration of waiting period between IN-OXT treatment and test as well as standardization of activity during waiting period, iii) measurement protocol of urinary and blood oxytocin levels.

Studies have administered different doses of IN-OXT (typically ranging from 12 IU to 40 IU; but some subjects received 8 IU, while others up to 80 IU based on body weight) and waiting periods after the treatment also vary (from no waiting period to 45 minutes). As to date there are no (pre-registered) replications of IN-OXT studies the effect of these methodological discrepancies is not yet known. However, there are some general differences across the results reported in dog IN-OXT studies that are indicative of the existence of such effects. For example some studies report a strong effect of repeated testing (carry-over effect; e.g. Kovács et al., in prep; Oliva et al., 2015), but others do not (e.g. Macchitella et al., in prep; Hernádi et al., 2015). Also, sex differences in the effect of oxytocin have been documented in some studies (e.g. Nagasawa et al., 2015; Kovács et al., 2016), but not in others (e.g. Kis et al., 2015). While there is no methodological consensus in human IN-OXT research either, several further confounding factors have been identified that are potentially relevant for dogs as well (Guastella et al., 2013). For example nasal anatomy has been found to influence absorption upon nasal spray administration, thus an easily administered technique to characterise anatomical differences in the nasal cavity might be necessary. In addition to active compounds (e.g. OXT) each nasal spray formulation includes different ingredients that can be described by chemical characteristics that all impact on absorption capacity (such as molecular weight, polarity, pH, chemical modification, lipophilicity, chemical form, polymorphism, pKa, solubility, dissolution rate, mucosal irritancy, osmolarity, and particle size), thus it might be useful to report all formula ingredients in scientific manuscripts. In addition head position, breathing as well as bottle design, insertion depth and administration

angle also have an influence.
Standardization in the measurement of peripheral OXT is also necessary in order to compare results from different studies. A difference of four magnitudes has been reported in mean baseline blood oxytocin levels of dogs with 0.1 ng/L (Odendaal & Meintjes, 2003) versus 155.8 pmol/L (Handlin et al., 2011) respectively[1]. High individual variation (and the presence of a few outlier values) might of course cause substantial differences in mean values, but a difference of this magnitude is more likely to be caused by the populations under study being considerably different and/or the methodologies used (HPLC versus immunoassay) yielding vastly different results. Some (McCullough et al., 2013) have already cautioned that commercially available (immunoassay) methods frequently used to measure peripheral oxytocin have been proven to lack reliability when used on unextracted samples of human fluids as they tag molecules in addition to OXT.
Apart from the above methodological concerns the results of dog oxytocin research have proved that this area continues to be promising and it holds the potential to contribute to our understanding of human-analogue social skills in dogs. Also, many interesting research questions remain open. Future studies should for example clarify the generalizability of results by investigating e.g. breed effects. The underlying mechanisms of individual differences in responsiveness to IN-OXT treatment (e.g. differences in the OXTR gene, baseline behaviour, sex, etc) should be explored in order to tackle the possibility to use this treatment for problem behaviours. These should be complemented by investigating dose- and repeated (chronic) treatment effects. The direct investigation of epigenetical modifications of the oxytocin system (e.g. methylation of the OXTR gene) should shed light on how early social experience influences behaviour. Together these results will further validate the dog as a model of human social cognition, not only at the behavioural but also at the physiological level.

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References

Beetz, A., Uvnäs-Moberg, K., Julius, H., Kotrschal, K., 2012. Psychosocial and psychophysiological effects of human-animal interactions: The possible role of oxytocin. Front Psychol 3, 1-15.

Bence, M., Elek, Z., Kis, A., Kubinyi, E., Lakatos, G., Miklósi, Á., Pergel, E., Rónai, Zs., 2013. Analysis of oxytocin receptor gene as putative component of social behavior in family dogs. Behav Genet 43, 509.

Bensky, M.K., Gosling, S.D., Sinn, D.L., 2013. The world from a dog' s point of view: A review and synthesis of dog cognition research. In: Brockmann, H.J., Roper, T.J., Naguib, M., Barrett, L., (Eds.), Advances in the Study of Behavior. Elsevier Inc: Academic Press, 209-406.

Campbell, A., 2010. Oxytocin and human social behavior. Personal Soc Psychol Rev 14, 281-295.

Carter, C.S., 2014. Oxytocin pathways and the evolution of human behavior. Annu Rev Psychol 65, 17-39.

Fiset, S., Plourde, V., 2015. Commentary: Oxytocin-gaze positive loop and the coevolution of human-dog bonds. Front Psychol 6, 1845.

Guastella, A.J., Hickie, I.B., McGuinness, M.M., Otis, M., Woods, E.A., Disinger, H.M., Chan, H-K., Chen, T.F., Banati, R.B., 2013. Recommendations for the standardisation of oxytocin nasal administration and guidelines for its reporting in human research. Psychoneuroendocrinology 38, 612-625.

Handlin, L., Hydbring-Sandberg, E., Nilsson, A., Ejdebäck, M., Jansson, A., Uvnäs-Moberg, K.,

[1] Oxytocin is a 1k Dalton protein with a molar weight of 1007.18734 g/mol, thus *ng* and *pmol* are the same magnitude.

2011. Short-term interaction between dogs and their owners: effects on oxytocin, cortisol, insulin and heart rate – An exploratory study. Anthrozoos 24, 301-315.

Handlin, L., Nilsson, A., Ejdebäck, M., Hydbring-Sandberg, E., Uvnäs-Moberg, K., 2012. Associations between the psychological characteristics of the human-dog relationship and oxytocin and cortisol levels. Anthrozoos 25, 215-228.

Hare, B., Tomasello, M., 2005. Human-like social skills in dogs? Trends Cogn Sci 9, 439-444.

Heinrichs, M., Dawans, B., von Domes, G., von Dawans, B., 2009. Oxytocin, vasopressin, and human social behavior. Front Neuroendocrinol 30, 548-557.

Hernádi, A., Kis, A., Kanizsár, O., Tóth, K., Miklósi, B., Topál, J., 2015. Intranasally administered oxytocin affects how dogs (Canis familiaris) react to the threatening approach of their owner and an unfamiliar experimenter. Behav Processes 119, 1-5.

Hernádi, A., Miklósi, B., Kanizsár, O., Kis, A., Miklósi, Á., Topál, J. . Oxytocin modulates how dogs (Canis familiaris) look at human emotional faces. An eye-tracking study. (In prep)

Kanizsár, O., Hernádi, A., Topál, J., 2012. Why does the dog choose the less amount of food reward? The priming effect of pre-sensitization with social stimuli. In: Proceedings of Canine Science Forum, 110.

Kekecs, Z., Szollosi, A., Palfi, B., Szaszi, B., Kovacs, K.J., Dienes, Z., Aczel, B., 2016. Commentary: Oxytocin-gaze positive loop and the coevolution of human-dog bonds. Frontiers in Neuroscience 10, 155.

Kis, A., Bence, M., Lakatos, G., Pergel, E., Turcsán, B., Pluijmakers, J., Vas, J., Elek, Zs., Brúder, I., Földi, L., Sasvári-Székely, M., Miklósi, Á., Rónai, Zs., Kubinyi, E., 2014a. Oxytocin receptor gene polymorphisms are associated with human directed social behavior in dogs (Canis familiaris). PLOS ONE 9, e83993.

Kis, A., Kanizsár, O., Gácsi, M., Topál, J., 2014b. Intranasally administered oxytocin decreases heart rate and increases heart rate variability in dogs. J Vet Behav Clin Appl Res 9, e15.

Kis, A., Hernádi, A., Kanizsár, O., Gácsi, M., Topál, J., 2015. Oxytocin induces positive expectations about ambivalent stimuli (cognitive bias) in dogs. Horm Behav 69, 1-7.

Kis, A., Hernádi, A., Virányi, Zs., Miklósi, Á., Topál, J. . Susceptibility to social priming is mediated through the oxytocin system in dogs, but not wolves. (In prep)

Kovács, K., Kis, A., Kanizsár, O., Hernádi, A., Gácsi, M., Topál, J., 2016. The effect of oxytocin on biological motion perception in dogs (Canis familiaris). Anim Cogn. (In press)

Kovács, K., Kis, A., Topál, J. . Differential effects of oxytocin on social sensitivity in two distinct breeds of dogs (Canis familiaris). (In prep)

Kovács, K., Park, S.Y., Hudecz, Á., Koller, D., Kanizsár, O., Kis, A., Gácsi, M., Rónai, Zs., Topál, J., Virányi, Zs. . Variation in the Oxytocin Receptor (OXTR) gene is associated with attachment style in Border Collie dogs. (In prep)

Kubinyi, E., Bence, M., Koller, D., Wan, M., Pergel, E., Balogh, L., Rónai, Zs., Sasvári-Székely, M., Miklósi, Á., 2016. Breed differences and genetic associations in dogs' greeting behavior towards humans? J Vet Behav Clin Appl Res. Revision submitted

Macchitella, L., Stegagno, T., Giaconella, R., Polizzi di Sorrentino, E., Schino, G., Addessi, E. . Oxytocin improves dogs' ability to follow informative pointing: a neuroemotional hypothesis. (In prep)

Maclean, B.E.L., Hare, B., 2015. Dogs hijack the human bonding pathway. Science 80, 16-17.

Marx, P., Arany, A., Ronai, Z., Antal, P., Sasvari-Szekely, M., 2011. Genetic variability of the oxytocine receptor: an in silico study. Neuropsychopharmacol Hungarica 13, 139-144.

McCullough, M.E., Churchland, P.S., Mendez, A.J., 2013. Problems with measuring peripheral oxytocin: can the data on oxytocin and human behavior be trusted? Neurosci Biobehav Rev 37, 1485-1492.

Miklósi, Á., Topál, J., 2013. What does it take to become "best friends"? Evolutionary changes in canine social competence. Trends Cogn Sci 17, 287-294.

Mitsui, S., Yamamoto, M., Nagasawa, M., Mogi, K., Kikusui, T., Ohtani, N., Ohta, M., 2011. Urinary oxytocin as a noninvasive biomarker of positive emotion in dogs. Horm Behav 60,

239-43.

Nagasawa, M., Mitsui, S., En, S., Ohatani, N., Ohta, M., Sakuma, Y., Onaka, T., Mogi, K., Kikusui, T., 2015. Oxytocin-gaze positive loop and the coevolution of human-dog bonds. Science 348, 333-336.

Odendaal, J.S.J., 1999. A physiological basis for animal-facilitated psychotherapy. PhD thesis, University of Pretonia.

Odendaal, J., 2000. Animal-assisted therapy — magic or medicine? J Psychosom Res 49, 275-280.

Odendaal, J.S.J., Meintjes, R.A., 2003. Neurophysiological correlates of affiliative behaviour between humans and dogs. Vet J 165, 296-301.

Oliva, J.L., Rault, J-L., Appleton, B., Lill, A., 2015. Oxytocin enhances the appropriate use of human social cues by the domestic dog (Canis familiaris) in an object choice task. Anim Cogn 18, 767-775.

Oliva, J.L., Rault, J-L., Appleton, B., Lill, A., 2016a. Oxytocin blocks pet dog (Canis familiaris) object choice task performance being predicted by owner-perceived intelligence and owner attachment. Pet Behaviour Science. (In press)

Oliva, J.L., Wong, Y.T., Rault, J-L,. Appleton, B., Lill, A., 2016b. The oxytocin receptor gene, an integral piece of the evolution of Canis familaris from Canis lupus. Pet Behaviour Science. (In press)

Park, S.Y., Kovács, K., Turcsán, B., Koller, D., Kanizsár, O., Kis, A., Gaugg, A., Virányi, Zs., Rónai, Zs., Topál, J., 2014. Association between oxytocin receptor gene polymorphisms and reaction to ambiguity in social situations in domestic dogs. In: Mills, D.S., Griffin, K., Finka, L., et al. (Eds.) Proceedings of the Canine Science Forum, Lincoln, UK, 96-97.

Quintana, D.S., Alvares, G., Hickie, I.B., Guastella, A.J., 2014. Do delivery routes of intranasally administered oxytocin account for observed effects on social cognition and behavior? A two-level model. Neurosci Biobehav Rev 1-11.

Rehn, T., Handlin, L., Uvnäs-Moberg, K., Keeling, L.J., 2014. Dogs' endocrine and behavioural responses at reunion are affected by how the human initiates contact. Physiol Behav 124, 45-53.

Romanciuc, F., Pop, R.M., Socaciu, C., 2014. Physiological effects of human-animal positive interaction in dogs — Review of the literature. Bulletin UASVM Animal Science and Biotechnologies, 71(2), 250-255.

Romero, T., Nagasawa, M., Mogi, K., Hasegawa, T., Kikusui, T., 2014. Oxytocin promotes social bonding in dogs. Proc Natl Acad Sci 111, 9085-9090.

Romero, T., Nagasawa, M., Mogi, K., Hasegawa, T., Kikusui, T., 2015. Intranasal administration of oxytocin promotes social play in domestic dogs. Commun Integr Biol 8(3), e1017157.

Somppi, S., Törnqvist, H., Koskela, A., Krause, C., Topál, J., Vainio, O., 2016. Nasal oxytocin administration enhances gazing at eyes of smiling humans in domestic dogs – preliminary results. In: Proceedings of the Canine Science Forum, Padova.

Thielke, L.E., Udell, M.A.R., 2015. The role of oxytocin in relationships between dogs and humans and potential applications for the treatment of separation anxiety in dogs. Biol Rev. (In press)

Tóth, K., Kanizsár, O., Topál, J., Kis, A. The effect of oxytocin on contagious yawning in dogs. (In prep)

Turcsán, B., Virányi, Z., Koller, D., Rónai, Zs., Range, F., 2014. Polymorphisms in the oxytocin receptor gene are associated with social behaviour in Border collies. In: Mills, D.S., Griffin, K., Finka, L., et al. (Eds.) Proceedings of the Canine Science Forum. Lincoln, UK, 302-303.

van Rooy, D., Haase, B., McGreevy, P.D., Thomson, P.C., Wade, C.M., 2016. Evaluating candidate genes oprm1, drd2, avpr1a and oxtr in golden retrievers with separation-related behaviors. J Vet Behav Clin Appl Res. (In press)

Yamasue, H., Yee, J.R., Hurlemann, R., Rilling, J.K., Chen, F., Meyer-Lindenberg, A., Tost, H., 2012. Integrative approaches utilizing oxytocin to enhance prosocial behavior: from animal and human social behavior to autistic social dysfunction. J Neurosci 32, 14109-14117.

- I11 - DEVELOPMENT OF EXPERTISE IN WORKING DOGS: THE ROLE OF SOCIAL AFFORDANCES

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Abstract:

While skill in dogs and people both require practice and experience to acquire, what role do genetics play? Physical morphology has a strong genetic component and this obviously plays a role in the development of physical skills, but cognitive skills? People rank breeds of dogs for trainability and intelligence with high consistency despite a lack of evidence of actual breed differences in underlying cognitive abilities. An alternative perspective is that people may use dog morphology to determine the intelligence of breeds. People may detect dog breeds' social affordances which are determined by the breeds' morphology. Breeds of dogs vary in morphological specialization with a continuum from being specialized for running (narrow headed) to being specialized for fighting (broad headed). Dogs at either extreme are unlikely to afford being trained for generalized tasks, as they are task specialists by form. In the present article I relay the findings of two simply studies where people rated photographs of dogs and drawings of the faces of dog-like avatars which were narrow, medium and broad shaped for intelligence, aggression, and anxiety. Despite being provided with no behavioral information, people consistently rated the medium shaped dogs as the most intelligent in line with the social affordance perspective. Perhaps, what is meant by cognitive differences are shapes that are easier or harder to train.

Keywords: *affordances; breed differences; expertise; intelligence; skill*

Introduction

Working dogs develop their skills in a manner similar to working people via an extended period of practice. Even in an activity which appears relatively simple, such as pulling a heavy weight, dogs improve dramatically with practice and experience. As an example the owner of Bridger a Swiss Mountain Dog was encouraged to compete by some friends in the sport of weight-pulling with Bridger. While Bridger had partook in skijoring, rollerjoring, and bikejoring and thus was used to pulling in a harness, he was novice to pulling heavy loads. The sport of weigh-pulling is an open event in which dogs pull the maximal load they can handle either on a wheeled cart or snow sled over a short distance. Weight-pulling would be the equivalent for dogs to the human strength sports such as powerlifting or strong-person events. Bridger's initial pull in a public weight-pulling competition was 1271 kg. A year and a month later Bridger pulled 1819 kg in a public competition, which represents a 43% gain on the initial public pull.

My interest in canine skill or expertise development, emerged from a vexing problem in the human expertise literature: the classic nature versus nurture debate. How much of eventual expertise is due to genetic contributions and how much is due to experience and practice? No one denies a role for both, but there is a question regarding the relative contribution of both. This debate is not as tractable in regards to people as it would be in regards to dogs (or other non-human animals), as we can control the genetics and early living conditions of dogs, but not people. This question prompted me to explore the topic as dogs appear to me to be experts (Helton, 2009).

Undoubtedly for a skill such as weight-pulling genetics plays an important role, as physical morphology is critical. For example, for their weight, the more brachycephalic (broad

headed) shaped mastiff breeds are much stronger than more dolichocephalic (narrow headed) husky breeds (Helton); those two types being the most commonly employed kinds of dogs in weight-pulling. Body shape plays a critical role for the development of physicals skills, but what about more cognitive skills or so-called intelligence differences in breeds. Are some dogs "smarter" than others and what does this mean in regards to dogs? This is where the story takes an interesting turn.

Cognitive Differences: Are We Really Talking About Social Affordances?

Breeds of dog (Canis lupus familiaris) are rated as differing in their perceived intelligence or trainability (Coren, 1994; Ley et al., 2009; Rooney & Bradshaw, 2004; Serpell & Hsu, 2005). There is high consistency in the ranking of dog breeds for their perceived intelligence and trainability both across and within studies. For example, in his survey of 208 North American dog obedience judges, Coren (1994) had judges rank the working intelligence of breeds of dog based on the judges' experiences in obedience competitions. The inter-rater reliability of these ratings was high, Cohen's kappa, k = 0.71 (Coren, personal communication). According to Landis & Koch (1977) a value this high, especially considering the total number of items being rated, is considered to reflect "substantial agreement."

The high reliability of breed rankings for differences in perceived trainability or intelligence is remarkable considering the lack of behavioral evidence in controlled studies indicating breeds actually differ in their cognitive abilities (Gagnon & Dore, 1992; Pongracz et al., 2004; Scott & Fuller, 1965). While not ruling out the existence of cognitive differences amongst dog breeds, I have discovered and purposed an alternative explanation (Helton, 2009, 2010). Instead of these ratings reflecting cognitive differences amongst breeds per se, the ratings may actually reflect differences in physical shape amongst breeds. These shape differences may affect the perceived quality of dogs for training and for their ability to perform various tasks. In contrast to the cognitive differences perspective, my perspective could be called the social affordances perspective. Affordances were proposed by Gibson (1979; 1986) to be the directly perceived environmental opportunities for action available to animals (for example, chairs are perceived by people to afford sitting). Essentially, objects afford or enable actions and animals should be attuned to perceive these action capabilities of objects. The term has been broadened by ecologically oriented psychologists to include the immediate perception of social action capabilities, hence, social affordances (Loveland, 1991; Reed, 1988). In the social affordances perspective, dogs with certain shapes would be perceived as being easier to train generally or for specific tasks because of an accurate appraisal of the fit between a dog's shape and task requirements, e.g. what the dog's shape socially affords. In particular, Helton suggests dog breeds that are rated particularly highly for their trainability are those that are neither specialized for running, such as sight-hounds, or fighting, such as mastiffs, but instead are a compromise between these two extreme body shapes.

Dogs' are classified as dolichocephalic (long skulls), mesocephalic (moderate skulls), or brachycephalic (broad skulls), based on calculated cephalic or skull index, a ratio between skull width and length. There is an underlying continuum between dolichocepahlic and brachycephalic with no natural breaks occurring in this continuum. Although there are no natural breaks in the continuum, the anatomies of dogs falling along the continuum are distinct, for example, Greyhounds which are more dolichocephalic and Staffordshire Bull Terriers which are more brachycephalic are anatomically distinct (Ellis et al., 2004; Kemp et al., 2005). Whereas Greyhounds are anatomically specialized for running, Staffordshire Bull Terriers are specialists for fighting or close quarter's engagements. Brachycephalic dogs' bodies are built to withstand the multi-directional forces of wrestling, whereas dolichocephalic dogs' bodies are built to withstand the directional forces of running (Kemp et al., 2005). When controlling for overall mass, brachycephalic dogs are overall stronger (Helton, 2011) and they can generate greater bite forces (Ellis et al., 2009). The anatomical specializations even extend to differences in sensory neurophysiology (McGreevy et al.,

2004). The functional trade-offs between morphology and running-fighting capability is common across species, as these functional trade-offs reflect the underlying realities of biomechanics (Wang & Tedford, 2008).
People can accurately assess the physical abilities of other people from both still body and facial photographs (Sell et al., 2009). People may also be able to assess dogs for intelligence and trainability by accurately assessing morphological differences in functional fit (task specialization). Indeed, intelligence ratings for dogs may be more about their physical morphology than their cognitive abilities. Non-specialists should be the most functionally flexible; hence, dogs more mesocephalic in shape should be perceived as more intelligent (and thus, trainable). This may partially explain people's ratings of intelligence in dogs. These features may also affect other perceptions of dogs by people. For example, dogs that can actually do more physical damage, such as more brachycephalic shaped dogs, may be automatically perceived as a potential threat (e.g. relatively more formidable), hence, may tend to be labeled aggressive. The trait label may simply reflect the detection of the dog's social affordance (what they are socially capable of), not an accurate assessment of the dog's behavioral disposition.

Demonstrations

In order to demonstrate people's perceptions, two studies will be related. In the first, people were asked to rate black and white photographs of dogs representing different shapes (more dolichocephalic, mesocephalic, and more brachycephalic) for intelligence, aggression and anxiousness. In the second study, people were asked to rate artificial dog face shapes or avatars, manipulating face width (3 levels) and ear positioning (erect, floppy). In the second study the avatars were simple 2 dimensional drawings (see Figure 1).
Hence, skull shape was not being represented but facial ratios (height to width), which may be another, albeit simpler, indicator of skull shape. This second study was used largely to see if the head shape findings of the first study would replicate with more controlled artificial stimuli, as pictures of real dogs entail more detail than just skull or head shape, and people may be familiar with social stereotypes about particular breeds.
For the dog pictures, twenty (16 women and 4 men) people participated in this study. They ranged in age between 20 and 39 years (M = 24.1, SD = 5.2). Thirteen of the 20 had previously owned a dog. The participants were given black and white grey-scaled photographs of the representative dogs taken from breed websites printed on white paper. The pictures were presented at random. The dog pictures consisted of more narrow headed dogs: Italian Greyhound, Greyhound, and Afghan hound; more medium headed dogs: Brittany spaniel, Border collie, and Labrador retriever; and more broad headed dogs: King Charles spaniel, American Bulldog, and Bull Mastiff. The breeds where chosen as they are fairly representative, covering a range of overall body sizes, while still being clearly classifiable into the three head shape groups based on breed standards (Gácsi et al., 2009). The participants were asked to rate the dogs given how they appeared in the photographs for the traits of aggressive, anxious, and intelligent. For each trait they were to respond using a 1 (strongly disagree) to 7 (strongly agree) scale to describe how much they agreed that the dog in the photograph had the trait in question. For example, if they agreed strongly that the dog looked intelligent then they would have marked down 7 on the sheet. The differences amongst the

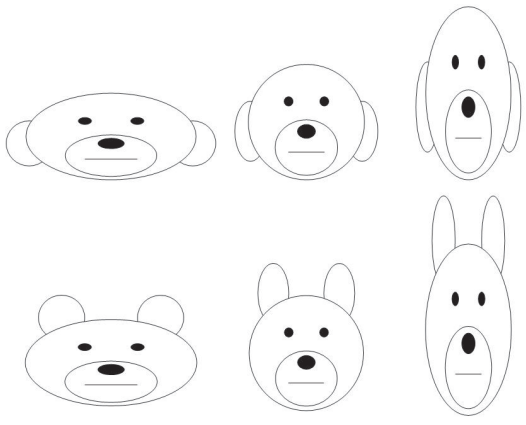

Figure 1. The avatars used in study 2.

individual photographs could be due to a combination of the specific individual represented, their specific pose, the breed, background, or nuances of the photograph itself (angle, lighting, etc.); therefore, averaging the ratings of the photographs for each of the three shapes was performed to mitigate some of these differences. In regards for aggression ratings, all three shapes were significantly different from each other ts(19) = 3.79-6.65, p = .001 (if conservatively corrected p < .017). In regards to intelligence, medium skull shape dogs were rated significantly more intelligent than the broad and narrow skull shape dogs, F(1,19) = 18.43, p < .001, but intelligence ratings of narrow and broad shaped dogs did not significantly differ, F(1,19) = 2.85, p = .108. The mean ratings for intelligence and aggression for the three shapes are presented in Figure 2 with standard errors of the mean.

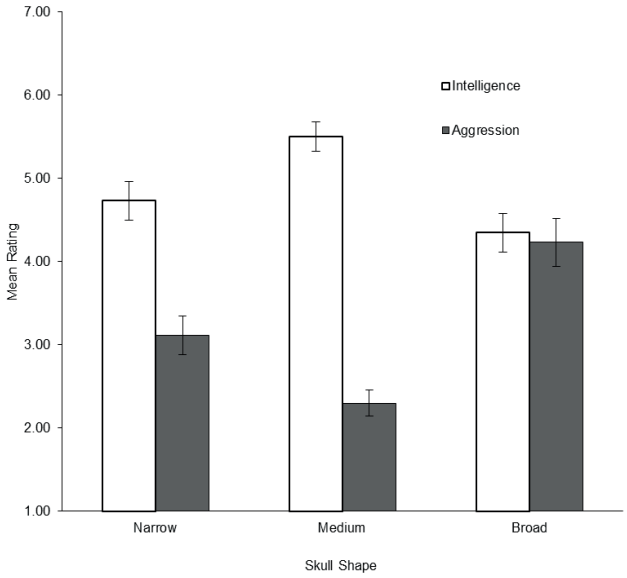

Figure 2. The mean intelligence and aggression ratings of the three skull shapes for the dog pictures (error bars are standard errors of the mean).

For the avatar (drawings), fourteen (6 women and 8 men) people participated in this study. They ranged in age between 20 and 26 years (M = 21.9, SD = 1.6). The participants were given black and white artificial figures of dog-like avatars (see Figure 1). The avatars represented three face shapes (tall-narrow, medium, and short-wide) and two ear positions (up and down). The avatars were presented in a random order for each participant. The participants were asked to rate the avatars given how they appeared in the drawings for the traits of aggressive, anxious, and intelligent. For each trait they were to respond using a 1 (strongly disagree) to 7 (strongly agree) scale to describe how much they agreed that the avatar in the drawing had the trait in question. For example, if they agreed strongly that the avatar looked intelligent then they would have marked down 7 on the sheet. There was a significant main effect for ear position for aggression, F(1,13) = 15.13, p = .002, with erect ears rated as more aggressive (M = 3.43) than down or floppy ears (M = 2.24). All other results were insignificant, p > .05. In the case of anxiousness, there was a significant shape by ear interaction, F(2,26) = 3.75, p = .037. The interaction is displayed in Figure 3.

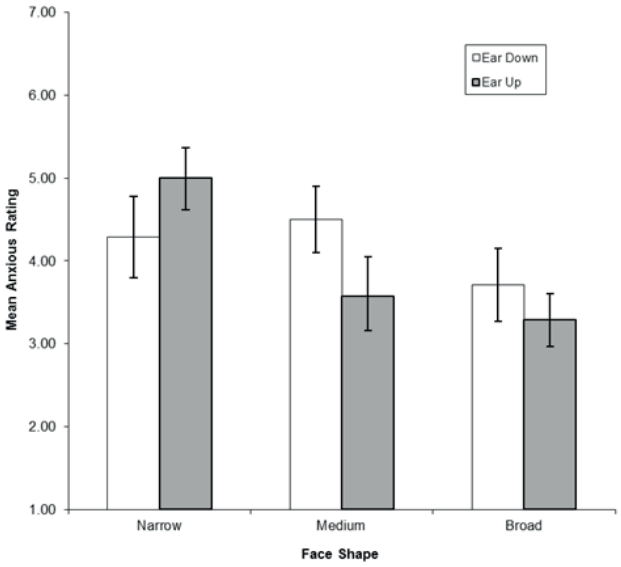

Figure 3. The mean anxiousness ratings of the three face shapes and two ear positions for the avatar pictures (error bars are standard errors of the mean).

For intelligence, there was a significant main effect for shape, F(2,26) = 12.23, p < .001. In regards to intelligence, medium face shape

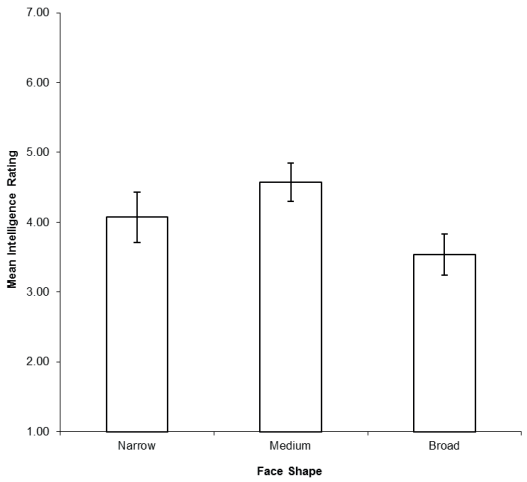

Figure 4. The mean intelligence ratings of the three face shapes for the avatar pictures (error bars are standard errors of the mean).

avatars were rated significantly more intelligent than the broad and narrow face shape avatars, $F(1,19) = 14.68$, $p = .002$, and broad shaped avatars were rated significantly less intelligent than narrow shaped avatars, $F(1,19) = 8.38$, $p = .013$. The mean ratings for intelligence for the three shapes are presented in Figure 4 with standard errors of the mean.

The intelligence ratings for the medium shaped dogs were indeed significantly higher than those for the narrow or broad shaped dogs. Considering the only information in the pictures where the general look of the dog and breed membership, this raises the question what information is being used by people to make their intelligence ratings. While in Coren's (1994) original study the breed ratings were made by individuals with significant experience with a variety of dogs (American and Canadian Kennel Club obedience judges), these ratings were made by relatively inexperienced individuals. Therefore the ratings are probably not being made based on behavioral or cognitive evidence for breed differences in dogs. Also it should be kept in mind that there is no existing evidence indicating there actually are any reliable or objective breed differences in cognitive ability (Gagnon & Dore, 1992; Pongracz et al., 2004; Scott & Fuller, 1965).

Conclusion

People are sensitive to the morphological shapes of dog breeds. Morphological shapes do differ between dog breeds and people can directly perceive these differences; they are perceptually obvious. Morphological shape does constrain action capabilities in dogs (Helton, 2011). Indeed, dogs bred to run extremely fast have been morphologically specialized by artificial selection specifically for this task. This specialization comes with morphological trade-offs. Also, dogs bred for their ability to dominate in fights have been morphologically specialized by artificial selection specifically for this task (historically, pit-bull terriers and mastiffs were bred to be gladiators and guards). Those dog breeds that are rated as highly intelligent are rated as such perhaps because they are relatively generically shaped. These dogs are balanced in the trade-off between running and fighting ability, and thus, may be the dogs that appear most readily trainable for a wide variety of non-specialized tasks (such as herding, detection work, obedience, etc.). The generic trainability may be labeled by people as intelligence, but it may not indicate any detected differences in cognitive abilities, but simply a convenient way to relay "good shape for lots of tasks."

The ability, for example, of people to make intelligence ratings from simple line drawings of avatars should also give some pause to those who believe people's ratings of dog breeds for intelligence are based primarily on behavioral or cognitive assessments. These avatars, being essentially two dimensional constructions, do not have any cognitive abilities and do not actually behave. So if intelligence ratings are determined by these attributes, how are people actually making the ratings? Perhaps they infer the line drawings are representative of real dogs, but looking at them some of the avatars do not seem to represent dogs very well, but look more like teddy bears (which also do not have cognitive abilities). Alternatively, perhaps, the drawings of the avatars trigger some morphological shape based social affordance detection. This affordance may be detected by simply using the invariants of face geometry.

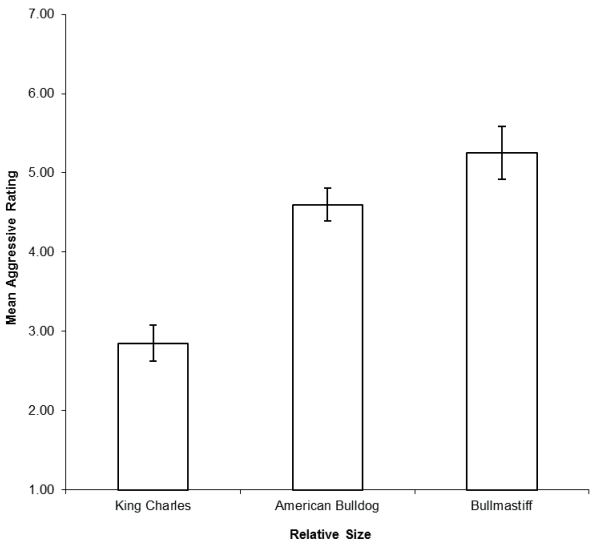

Figure 5. The mean aggressive ratings of the three dog pictures ranked by relative size for the wide skulled dogs (error bars are standard errors of the mean).

Essentially, people may be attuned to detect the social affordances of dogs. A dog's shape conveys information about the dog's action capabilities for the dog's interactions with people, other animals, and the dog's environment. The trait labels given by people may be partially explained as their verbalization of these detected social affordances. This social affordance perspective may help explain other judgments or ratings made by people of dog breeds. For example, aggression ratings may also be influenced by morphology. Broad (brachycephalic) shaped dog pictures were rated as more aggressive than the other dogs. While this may reflect simply a stereotype based on the bad press many of these kinds of dogs have recently had, the rating may also be based on the detection of the action capabilities of these dogs. The amount of damage a dog can physically do is actually constrained by the dog's shape. Broad shaped dogs have been artificially selected as combatants. Their physical shape affords their ability to dominate their opponents in fights. They are for their weight physically stronger (Helton, 2011) their skeletons are more robust (Kemp et al., 2005), and for their weight they can generate stronger bite forces (their teeth are closer to the hinge point; Ellis et al., 2009). Indeed even their visual physiology is specialized for focusing on central targets (McGreevy et al., 2003). Thus, for these dogs their bodies may afford physical aggression.

Lending some evidence to this perspective, the broad shaped dog pictures can be compared across their respective sizes. As displayed in Figure 5, relative size may also matter for ratings of aggression in these dogs and is topic for future planned investigations.

Increases in size would facilitate the amount of physical damage these dogs could inflict in social interactions. If aggression ratings are based on an assessment or detection of the dog's damage inflicting capability (based on morphology), dogs like American Bulldogs, Staffordshire Bull Terriers (especially the bigger American versions), Bullmastiffs, Rottweilers, Tosas, etc. that are both broad and big should be labeled as aggressive breeds. Not surprisingly they are, despite the fact that behaviorally-speaking the vast majority of the members of these breeds will never bite anyone (Collier, 2006). This is not to say these dogs do not fundamentally differ in temperament, but simply the social affordance theory may provide an alternative perspective worth considering. When a person seeks an aggressive looking dog, perhaps what they are selecting for is simply the ability of the dog to inflict damage (not temperament per se). Then they may coax this animal by treatment and training into what they are seeking: a weapon. However, let us assume you blamed the dog's breed for the outcome, for example claiming the breed is temperamentally disposed to aggression, and wholesale banned the breed. If some people, however, are detecting the ability of the dog to afford harm, they may simply choose the next best dog that affords harm. If you ban knifes and the person is seeking to inflict harm, any sharp pointy object may suffice (although arguably you may make the affordance more difficult to exploit). In a bar room brawl broken beer bottles can quickly afford stabbing. Thus if you ban "dangerous" breeds those folks may simply pick the next dog breed that affords harm infliction and that breed will become the next dangerous breed and so on, until we end up having no pet dogs

at all (or at least none weighing more than 25 kg). Of course this is not a political commentary on proposed bans of possible weapons, only a different perspective which may see the root of the problem lying at a different level. For example, the particular dog breeds may not in of themselves be the problem, but instead they are the means through which people may act because they are correctly perceived as having the proper social affordances.

References

Alpak, H., Mutuş, R., Onar, V., 2004. Correlation analysis of the skull and long bone measurements of the dog. Annals of Anatomy-Anatomischer Anzeiger 186(4), 323-330.

Arhant, C., Bubna-Littitz, H., Bartels, A., Futschik, A., Troxler, J., 2010. Behaviour of smaller and larger dogs: Effects of training methods, inconsistency of owner behaviour and level of engagement in activities with the dog. Applied Animal Behaviour Science 123(3), 131-142.

Collier, S., 2006. Breed-specific legislation and the pit bull terrier: Are the laws justified? Journal of Veterinary Behavior: Clinical Applications and Research 1(1), 17-22.

Coppinger, R., Coppinger, L., 2001. Dogs: A startling new understanding of canine origin, behavior & evolution. Scribner: New York.

Coren, S., 1994. The intelligence of dogs. New York: Bantam.

Ellis, J.L., Thomason, J., Kebreab, E., Zubair, K., France, J., 2009. Cranial dimensions and forces of biting in the domestic dog. Journal of anatomy 214(3), 362-373.

Gagnon, S., Dore, F.Y., 1992. Search behavior in various breeds of adult dogs (Canis familiaris): Object permanence and olfactory cues. Journal of Comparative Psychology, 106(1), 58-68.

Gácsi, M., McGreevy, P., Kara, E., Miklósi, Á., 2009. Effects of selection for cooperation and attention in dogs. Behavioral and Brain Functions 5(1), 31.

Gibson, J.J., 1986. The ecological approach to visual perception. Hillsdale, NJ: Lawrence Erlbaum Associates, Inc. (Original work published 1979)

Helton, W.S., 2009. Cephalic index and perceived dog trainability. Behavioural Processes 82(3), 355-358.

Helton, W.S., 2010. Does perceived trainability of dog (Canis lupus familiaris) breeds reflect differences in learning or differences in physical ability? Behavioural Processes 83(3), 315-323.

Helton, W.S., 2011. Performance constraints in strength events in dogs (Canis lupus familiaris). Behavioural Processes 86(1), 149-151.

Kemp, T.J., Bachus, K.N., Nairn, J.A., Carrier, D.R., 2005. Functional trade-offs in the limb bones of dogs selected for running versus fighting. Journal of experimental biology 208(18), 3475-3482.

Landis, J.R., Koch, G.G., 1977. The measurement of observer agreement for categorical data. Biometrics 159-174.

Ley, J.M., Bennett, P.C., Coleman, G.J., 2009. A refinement and validation of the Monash Canine Personality Questionnaire (MCPQ). Applied Animal Behaviour Science 116(2), 220-227.

Loveland, K.A., 1991. Social affordances and interaction II: Autism and the affordances of the human environment. Ecological Psychology 3(2), 99-119.

McGreevy, P., Grassi, T.D., Harman, A.M., 2003. A strong correlation exists between the distribution of retinal ganglion cells and nose length in the dog. Brain, Behavior and Evolution 63(1), 13-22.

Miklosi, A., 2007. Dog: Behaviour, evolution, and cognition. Oxford: Oxford University Press.

Pongrácz, P., Miklósi, Á., Vida, V., Csányi, V., 2005. The pet dogs ability for learning from a human demonstrator in a detour task is independent from the breed and age. Applied Animal Behaviour Science 90(3), 309-323.

Reed, E.S., 1988. The affordances of the animate environment: Social science from the ecological point of view. In: Ingold, T., (Ed.), What is an animal? London: Allen & Unwin, 110-126.

Rooney, N.J., Bradshaw, J.W., 2004. Breed and sex differences in the behavioural attributes of specialist search dogs—a questionnaire survey of trainers and handlers. Applied Animal Behaviour Science 86(1), 123-135.

Ruxton, G.D., Beauchamp, G., 2008. Time for some a priori thinking about post hoc testing. Behavioral Ecology 19(3), 690-693.

Scott, J.P., Fuller, J.L., 1965. Genetics and the social behavior of the dog. Chicago: Chicago University Press.

Sell, A., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., Gurven, M., 2009. Human adaptations for the visual assessment of strength and fighting ability from the body and face. Proceedings of the Royal Society B: Biological Sciences 276(1656), 575-584.

Serpell, J.A., Hsu, Y., 2005. Effects of breed, sex, and neuter status on trainability in dogs. Anthrozoos, 18, 196-207.

Wang, X., Tedford, R.H., 2008. Dogs: Their fossil relatives and evolutionary history. New York: Columbia University Press.

Warden, C. J., Warner, L.H., 1928. The sensory capacities and intelligence of dogs, with a report on the ability of the noted dog "Fellow" to respond to verbal stimuli. The Quarterly Review of Biology 3(1), 1-28.

- I12 - SPECIES CONSERVATION WITHOUT BOUNDARIES: WOLVES AND HUMANS IN EUROPE?

Luigi Boitani* (presenting)

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Abstract:

In Europe, and particularly in Italy, wolves are increasing in number and distribution areas, and are often in close contact with human activities. I will present the most recent data on wolf numbers and ranges for all European countries as well a summary of the recent improvements toward management at population instead that at country level. The positive trends in Italy have been favoured by the general abandonment of marginal agriculture and widespread increase of wild preys such as deer and wild boar. The nature and level of conflict with human activities change across the continent and different approaches and tools are necessary to manage wolves in various ecological and socio-economic contexts. The overall goal set by the Large Carnivore Initiative for Europe (an IUCN/SSC Specialist Group) is "To maintain and restore, in coexistence with people, viable populations of large carnivores as an integral part of the ecosystems and landscapes across Europe". This implies extensive coexistence with human activities. Throughout most of Europe, the coexistence of wolves and humans (inside and outside protected areas) is already fairly common and it is encouraged by setting clear management goals and through the implementation of effective means to prevent and mitigate the conflicts. However, coexistence with human activities also implies acceptance that wolves may not be allowed to express the full range of their ecological roles, as human intervention may be necessary to control the natural ecological patterns toward socially and economically acceptable compromises.

Keywords: *coexistence; Habitat Directive; human-carnivore conflict; wolf*

Round Table on Service Dogs

- RT1 - TECHNICAL APPROACHES AND CHALLENGES TO SERVICE DOG TRAINING

Selina Gibsone* (presenting)

Dogs for the Good, United Kingdom.
**Corresponding author: selina.gibsone@dogsforgood.org*

This presentation will focus on the technical approaches and challenges common to service dog training.
The two core elements that contribute to the effective training of a service dog will be considered: the wide range of tasks to assist people with different disabilities and needs; and, importantly, general behaviour in public spaces, which helps to support access rights.
The challenges for the dog and trainer of recognised socialisation and training techniques will be examined; where a combination of volunteers and staff are engaged in the training of service dogs before they are matched and placed with clients. This will include the implications of dogs being required to form relationships with multiple handlers/trainers and also the specific skills required of trainers in managing this and adapting their approach to each dog.
The factors growing organisations should consider in designing a system to increase the number of trained dogs they can deliver to clients will also be considered, while ensuring that each dog's needs are fully supported in this process. This will include implications for dog sourcing and selection for the service dog work. The approaches and potential issues in creating a solid working partnership between client and dog will also be discussed, with a particular focus on individual client training and aftercare support.

Keywords: *dog-human relationship, service dogs, training*

- RT2 - SERVICE DOGS: OPPORTUNITIES AND SCIENTIFIC QUESTIONS

Ádám Miklósi* (presenting)

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Some dogs were always around to help humans in various activities. Their fate depends on the societal changes in humans. It started with dogs for the blind person, and police dogs but today many hundreds of dog are trained every day for working as an assistant dog for disabled people, people living with auditory impairment, but dogs play a vital role in animal assisted therapies. In addition, individual helper dogs are becoming also more popular who are trained specifically for the person in need for any kind of physical, social or emotional help. Many enthusiastic dog people, often self-made dog trainers educate these dogs and their prospective owners. There is, however, only very narrow common ground of knowledge that could be used as a basis (e.g. 'clicker training'). Canine science could help to establish a knowledge base that could provide input for all those who are open to improve dog training.
The round table offers a possibility to discuss the relationship between the training of service dogs and current applied methods and scientific knowledge.
(1) Is there a need for some basic knowledge on service dog training that are shared by all present and prospective trainers world wide?
(2) What are the best practices to select dogs for such specific training? Why do so many dogs fail? Could selective breeding help in this case?
(3) What are the best methods for training? To what extend should training depend on the individual? Why are social learning methods spreading so slow?
(4) Could we learn about dogs' mental capacities by testing service dogs? Are they 'special' (more intelligent) in any way, or 'just' trained in extraordinary manner?
(5) Is there a possibility to involve more mix-breed (shelter etc.) dogs in these training programs?
(6) What welfare issues should be taken seriously? How could we collect objective evidence?

Keywords: *dog training; intelligence; service dogs; welfare*

- RT3 - SERVICE DOGS: ETHICAL ASPECTS

Peter Sandøe[1],[2]* (presenting), Iben Meyer[3]

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For many people in the Western World, dogs are primarily viewed as friends and members of the family. Therefore, the idea of using dogs merely as a means to provide services to humans can produce negative reactions. Moreover, concerns have been put forward about the physical and mental welfare of service dogs. In this presentation, we will try to situate the discussion of using dogs to provide service and assistance to disabled people within a broader ethical context. Furthermore, we will suggest a framework for a forward-looking ethical discussion. The ethical context and framework both originate from discussions of the use of animals for research. The broader ethical context will be the idea of harm-benefit analysis where an activity is ethically assessed, based on a weighing of the potential harm to the affected animals against the likely benefits to both humans and animals. The suggested framework for forward-looking discussions consists of the two last of the so-called three Rs (Reduce, Replace, and Refine), which today are central to all discussions regarding the use of animals for research. In the case of service dogs the idea of Replacement relates to the question: Given advances in technology, notably robotics and information technology, is it possible to find alternatives to specific forms of use of service dogs? And Refinement is linked to the question: Is it possible to improve the way service dogs are trained and looked after in a way that minimizes negative consequences for their welfare?

Keywords: *assistance dogs, ethics, harm-benefit analysis, service dogs, three Rs*

- RT - Discussion

MODERATOR:

Emanuela Prato Previde Albrisi Colomban

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DISCUSSANTS:

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Karl Weissenbacher
Messerli Research Institute, University of Veterinary Medicine, University of Vienna, Austria.

Oral Presentations

- O1 - GLOBAL MOTION DETECTION IN DOGS (Canis Familiaris)

O. Kanizsár[1]* (presenting), P. Mongillo[1]; G. Campana[2], L. Battaglini[2] , P. Sambugaro[1], A. Scandurra[1], L. Marinelli[1]

[1]Laboratory of Applied Ethology, Department of Comparative Biomedicine and Food Science, Università degli Studi di Padova, Italy; [2]Department of General Psychology, Univeristà degli Studi di Padova. Italy.
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Highlights:

The aim of our study was to define thresholds of global motion perception in dogs. Dogs discriminated stimuli with different percentage, lifetime and density of coherently moving dots. Compared to other species, dogs' threshold of global motion perception is similar or higher.

Keywords: *discrimination task; dog; global motion; perception; threshold*

Motion perception is one of the main properties of the visual system. Although characteristics of this ability are well studied in humans, there is no data about dogs' sensitivity in detecting global motion. The aim of our study was to define thresholds of global motion perception in dogs and to investigate how features of the stimulus affect such threshold. The procedure was based on discrimination tasks where subjects had to discriminate between two stimuli presented on touch screens, representing kinetograms with different percentages of coherently moving dots. Three pet dogs participated in three experiments. Before each experiment subjects were trained to discriminate a positive stimulus (80% of coherently moving dots) from a negative one (0% of coherently moving dots). Afterwards, dogs underwent three tests (each containing 200 trials) varying the percentage of coherence (Exp 1), the density (Exp 2) and the lifetime of the dots (Exp 3). Results of Exp 1 show that the threshold of global motion perception varies between 36.1% and 39.0%. Decreasing dot density (Exp 2) had a great negative impact on the performance of the subjects, while decreasing dot lifetime (Exp 3) did not affect it. Dogs' perception threshold of global motion is similar or higher than in other species (e.g. cats, seals and humans) that have been tested in similar experimental conditions. This questions the general claim on dogs' higher performance in perceiving motion.

- O2 - DOGS´ DISCRIMINATION OF HUMAN SELFISH AND GENEROUS ATTITUDES: A COMPARISON OF FAMILY DOGS, SHELTER DOGS AND PUPPIES

F. Carballo[1],[2]* (presenting), M. Bentosela[1], V. Dzick[1], E. Freidin[1],[3]

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Highlights:

After 12 trials, family dogs reliably discriminate between humans who have been generous or selfish in food exchanges with them. We studied the role of socialization in the development of this skill by testing shelter dogs and puppies. We found that all dogs tested readily make this discrimination successfully, thus suggesting that the social skill involved develops early and does not require an intense previous social experience.

Keywords: *direct reciprocity; pet dogs; puppies; reputation; shelter dogs; social cognition*

Discrimination of and memory for others' generous and selfish behaviors could be adaptive abilities in social animals. Dogs have seemingly expressed such skills in both direct and indirect interactions with humans. However, it is not known whether these abilities require extensive social interaction with humans to be properly expressed. To answer this, we compared adult family dogs (i.e., well-socialized subjects), adult shelter dogs (i.e., poorly socialized subjects), and puppies between 45 and 60 days old (i.e., subjects that are in the process of socialization) in a task in which they were exposed to a generous and a selfish experimenter (GE and SE, respectively). During training, the GE would make a pointing gesture towards a bowl with hidden food, and then allowed the subject to eat the food, whereas the SE would make the pointing gesture but would not allow the subject to access the food. After 6 training trials with each experimenter, subjects were presented with a choice between the GE and the SE. We also ran a second set of training trials and a second choice test. Family and shelter dogs chose the GE over the SE above chance levels after the first set of training trials (binomial tests, *P*s<0.05). Puppies reliably chose the GE only after the second set of training trials. These findings suggest that the social skills needed to make the discrimination between generous and selfish people develop early in dogs and does not require an extensive previous social experience with humans.

- O3 - HUMAN AUTISM GENE ASSOCIATED WITH DOG-HUMAN COMMUNICATION AND SOCIALITY IN DOGS

M.E. Persson (presenting), D. Wright, L.S.V. Roth, P. Batakis, P. Jensen*

AVIAN Behaviour Genomics and Physiology Group, IFM Biology, Linköping University, Sweden;
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Highlights:

Dogs were tested using the "unsolvable problem" paradigm. Their human-directed contact seeking behaviors were analyzed. Genome-Wide Association Analysis revealed five candidate genes associated to these behaviors. These genes have previously been associated to social disorders in humans.

Keywords: *behavior genetics; candidate genes; genome-wide association study; inter-species communication; sociability*

Unlike their ancestors, dogs have evolved unique social skills allowing them to communicate and cooperate with humans. Previously, we found a significant heritability for variation in human-directed social behaviors in laboratory beagles (Persson et al., 2015). Therefore, the aim of the current study was to identify candidate genes associated with this variation. To do this, a Genome-Wide Association Study (GWAS) was performed on human-directed social behaviors filmed during the "unsolvable problem" paradigm. We recorded the propensity for dogs to initiate physical interactions with an unknown human while attempting to solve an unsolvable problem. Genotyping was done with a HD Canine SNP-chip on 190 beagles from a unique laboratory population, bred, kept and handled under highly standardized conditions. This revealed a genetic marker on chromosome 26 within the *SEZ6L* gene, significantly associated with time spent close to the human ($p=4.87x10^{-8}$; $R^2=0.15$) and in physical contact with the human ($p=5.25x10^{-7}$; $R^2=0.13$). Another suggestive locus on chromosome 26 within the *ARVCF* gene was also identified ($p=7.94x10^{-7}$; $R^2=0.14$) and three additional genes, including the *COMT* gene, were present in the same linkage block. In humans, the *SEZ6L* gene has previously been associated with autism and the *COMT* gene has been associated with aggression in adolescents with ADHD, all of which affects social abilities. This is, to our knowledge, the first genome-wide study to present candidate genes for dog sociality and inter-species communication.

References

Persson, M.E., Roth, L.S.V., Johnsson, M., Wright, D., Jensen, P., 2015. Human-directed social behaviour in dogs shows significant heritability. Genes Brain Behav 14, 337-344.

- O4 - HOW CAN WE TEST CANINE OLFACTORY CAPACITY? COMPARING DOG BREEDS AND WOLVES IN A NATURAL DETECTION TASK

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Highlights:

There is no standard test for assessing canine olfactory ability. We created a simple procedure that requires no pre-training to measure canine olfactory capacity. Scent breeds and wolves performed better than short-nosed or non-scent breeds in our olfactory test. The Natural Detection Task was efficient in quantifying and comparing dogs' olfactory abilities.

Keywords: *canine; dog; olfactory ability; olfactory testing; scent breeds; wolf*

Many breeds are bred specifically for increased performance in scent-based tasks. Whether such breeds have higher olfactory capacities has not yet been studied. Indeed, there is no standard test for assessing canine olfactory ability. This study aimed to create a simple procedure that requires no pre-training to measure differences in olfactory capacity across four groups of canines: (1) dog breeds selected for scenting ability; (2) dog breeds bred for other purposes; (3) dog breeds with exaggerated short-nosed features; and (4) hand-reared grey wolves. The procedure involved baiting a container with meat and placing it under one of four identical pots. Subjects were led along the row of pots and were tasked with determining by olfaction alone which of them contained the bait. There were five levels of increasing difficulty determined by the number of holes on the container's lid. A subsample of both dogs and wolves was retested to assess reliability. Breeds selected for scent work performed better than both short-nosed ($t_{(2,46)}$=3.621, p=0.002) and non-scent breeds ($t_{(2,46)}$=2.569, p=0.053). In the most difficult level, wolves (p=0.018) and scenting breeds (p=0.004) performed better than chance, while non-scenting and short-nosed breeds did not. In the retested samples wolves improved their success ($F_{(1,10)}$=6.557, p=0.028); however, dogs showed no change in their performances indicating that a single test is reliable enough to assess their capacity. We revealed measurable differences between dog breeds in their olfactory abilities and suggest that the Natural Detection Task is a good foundation for developing an efficient way of quantifying them.

- O5 - FUNCTIONAL UNDERSTANDING OF EMOTIONAL EXPRESSIONS IN DOMESTIC DOGS

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Highlights:

We analyzed mouth-licking behavior of dogs in a cross-modal emotion recognition paradigm. Mouth-licking occurred more in male subjects and towards human stimuli. The behavior was more frequent when dogs were looking at the angry face or turned their heads away from the screens. The findings suggest dogs have a functional understanding of emotional expressions.

Keywords: *dogs; emotion perception; emotion understanding; social cognition*

Dogs can discriminate and categorize emotional displays, however little is known about their ability to respond to emotions in a functional way. In a cross-modal preferential looking paradigm, we presented 17 adult family dogs with pairs of images of the same individual combined with a sound that could be positive, negative or neutral. Dogs matched the congruent audiovisual stimuli regardless of gender, valence or presentation side; evidence of the cognitive processing of facial expressions and vocalizations of both dogs and humans (Albuquerque et al., 2016). To assess whether dogs can functionally respond to emotions, other behavioral responses must be examined. Therefore, we coded the mouth-licking behavior (communicative signal in dogs in the absence of food) during stimuli presentation. We used a GLMM to analyze the intensity of mouth-licking in relation to time spent looking at the images (per trial) and an ANOVA to analyze the frequency of mouth-licking directed to the angry or happy face, center or away from the screens ("out") per dog. We found that mouth-licking occurred more in male subjects ($F_{1,48}$=3.892, p=0.054) and towards human stimuli ($F_{1,48}$=4.566, p=0.038). There was a significant effect of the direction dogs were looking at when they displayed mouth-licking ($F_{3,64}$=6.502, p=0.001) with higher frequency when looking at negative faces and out than towards happy or center (AngryXHappy: p=0.030; OutXHappy: p=0.051; AngryXCenter: p<0.001; OutXCenter: p=0.001; AngryXOut: p=0.821; HappyXCenter: p=0.113, LSD). Our results show a spontaneous differential behavioral response towards negative valence and so suggest a functional understanding of emotional information by the dogs.

References

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., Mills, D., 2016. Dogs recognize dog and human emotions. Biol Lett 12, 20150883.

- O6 - DIFFERENCES IN BEHAVIORAL FLEXIBILITY BETWEEN LONG-TERM DOG OWNERS, DOG ADOPTERS, AND DOG RELINQUISHERS

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Highlights:

A measure was adapted to assess behavioral flexibility in dog owners, adopters and relinquishers. It was administered to a sample of each population (n=554, n=100, n=621, respectively). Six items reliably distinguished between the long-term owners and relinquishers. These items appear to be a robust tool for highlighting at-risk dog adopters.

Keywords: *adopter; dog; owner; rehoming; relinquisher*

As in any personal relationship, conflict between dog and owner is inevitable, and a major reason for dog relinquishment is a failure to resolve such conflict. An owner's ability to resolve conflicts is a significant predictor of the likelihood of the dog being relinquished, and an owner's conflict resolution potential is a function of their level of behavioral flexibility in relation to accommodating their dog's needs. Two versions of a measure originally used to place human foster children into families (Doelling & Johnson, 1990) were adapted to be relevant to the dog-owner relationship, the DOTS-R ADULT and the CAES. Both were administered to three samples: long-term dog owners, dog adopters, and dog relinquishers. Item to total score bivariate correlations were conducted for the DOTS-R ADULT, and item to total factor score bivariate correlations were conducted for the CAES. Independent t-tests were conducted for the scales to assess differences in group means. The DOTS-R ADULT could not assess flexibility with confidence, so it was determined to be unreliable. Six items on the CAES were reliable, and could discriminate between owners and relinquishers. Using these items, statistically significant differences between the two samples were found ($p<0.05$). Therefore, these items can be used as a tool to identify adopters at increased risk of future dog relinquishment. It is imperative that characteristics of adopters and dogs increasing risk of relinquishment be considered when making placements; this research has re-conceptualized what these factors are by understanding that the dog-adopter relationship is dynamic and constantly evolving.

Acknowledgement: Dogs Trust

References

Doelling, J.L., Johnson, J.H., 1990. Predicting success in foster placement: The contribution of parent-child temperament characteristics. American Journal of Orthopsychiatry 60(4), 585-593.

- O7 - UNCONDITIONED ANXIETY IN DOMESTIC DOGS WITH OR WITHOUT BEHAVIOR PROBLEMS

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Highlights:

Pet dogs were recruited into two groups; affected or unaffected by behavior problems. Appetite, open field behavior and noise stimulus response were measured. Affected dogs displayed increased hyponeophagia and panting during noise stimulus compared to unaffected dogs. The unaffected hyponeophagic dogs displayed increased panting and increased noise aversion compared to normal unaffected dogs.

Keywords: *anxiety; behavior; dog; hyponeophagia; open field*

Anxiety is currently believed to play a central role in a range of behavior problems in dogs. Pet dogs aged 18 months to 8 years old from a range of breeds were assessed using a standardized owner questionnaire to categorize the number and severity of behavior problems. Dogs were recruited if they scored very high (affected, n = 37) or very low (control, n=38) on the questionnaire. Dogs were subjected to an appetite test, a 10-minute open field test and a 3-minute noise stimulus test. Affected dogs displayed more hyponeophagia (57%,SE = 8.1%) compared with control dogs (26%,SE = 7.1%, $\chi 2 = 0.015$) in the open field, and increased levels of panting (P = 0.024) during the noise stimulus. Within the control group, the dogs that displayed hyponeophagia had elevated panting during the open field (P = 0.009) and increased noise aversion during the second (P = 0.027) and third (P = 0.034) minutes of the noise stimulus compared with control dogs that ate the treat. These differences were not present within the affected group. Subsequent analysis excluded the hyponeophagic control dogs, producing an absolute control group. Compared with the absolute control dogs, the affected dogs travelled further (P = 0.039) and panted more (P = 0.044) during the open field test, panted more during the noise stimulus (P = 0.008), and displayed greater noise aversion (P = 0.033). These findings provide direct evidence that pet dogs with behavior problems often have increased levels of unconditioned anxiety compared with unaffected dogs.

- O8 - PLAYFUL ACTIVITIES POST-LEARNING IMPROVE MEMORY CONSOLIDATION IN LABRADOR RETRIEVER DOGS (Canis Lupus Familiaris)

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Highlights:

Enhancement of memory consolidation in dogs through post learning activities was investigated. Playful activity post learning improved memory recall in an object discrimination paradigm. Salivary cortisol significantly decreased after 30 minutes of play when compared to a control group. Further studies are important to evaluate future implications for the field of dog training.

Keywords: *activity; dog; memory consolidation; rest*

Situations that are emotional and arousing have an effect on cognitive performance. It is thought that beta-adrenergic activation and the release of specific stress hormones enhance memory consolidation and lead to an increase in memorability through facilitation of memory recall.
This has been shown in humans, non-human primates and rodents. Techniques which could enhance memory for tasks would be valuable, especially in dogs, which are extensively trained to aid humans.
A pseudo-randomized, counterbalanced, between subject study design was utilised and 16 Labrador Retrievers were trained in a 2-choice discrimination paradigm. After task acquisition, either a playful activity (PA) intervention (N=8) or a resting period (N=8) took place.
A range of factors including age, sex, training experience and trials to criterion on each day was subjected to a multiple factor/covariate General Linear Model analysis. The results show that PA post-learning improved memory consolidation as evidenced by fewer trials needed to re-learn the task 24 hours after initial acquisition (PA group: mean number of trials 26, SD 6; resting group: mean number of trials 43, SD 19, effect size 1.2). Average heart rate, as a measure of arousal, during intervention was significantly higher in the PA group (143 beats/min, SD 16) versus the resting group (86 beats/min, SD 19, $P<0.001$). Salivary cortisol did not significantly differ between groups during training, however a significant decrease ($p=0.02$, T: -2.9) was seen after PA.
To our knowledge this is the first evidence that post training activity may influence memory in dogs.

- O9 - NEURAL MECHANISMS FOR VERBAL PRAISE PROCESSING IN DOGS

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Highlights:

We used fMRI to study how dog brains segregate and integrate human speech cues. Dogs show a left hemisphere bias for processing words that are meaningful to them. Intonational cues are processed independently of word meaning in dogs' right hemisphere. Verbal praises elicit reward response in dogs only if both word meaning and intonation fit.

Keywords: *dog; fMRI; lateralization; reward; speech processing*

In human speech, communicative content is determined by what we say and how we say it. Lexical and intonational cues are processed in separate cortical pathways in humans, with left and right hemisphere biases respectively, and the neural integration of these cues is an important characteristic of linguistic processing. Human vocal social signals are highly relevant for dogs, but dog neural mechanisms to infer meaning from speech are unknown. Here we investigated for the first time, using fMRI, whether and how dog brain segregates and integrates lexical and intonational information in speech, specifically in verbal praises. Distinct neural activity patterns were identified for analysing word meaning and intonation. We found a left-hemisphere bias for processing meaningful words, corroborating recent behavioural findings on dog auditory lateralization ($F(1,12)=6.36$, $p=0.027$). Sensitivity to intonation was found in the same right auditory cortex subregion that had been shown to process emotional valence cues for non-speech vocalizations ($T(12)=4.34$, $p(corr)=0.041$). In ventral tegmental and caudate areas, we found activity increase only when both word meaning and intonation were consistent with a praise (ventral tegmental area: $T(12)=4.67$, $p(corr)=0.015$; left/right caudate: $T(12)=4.29/5.50$, $p(corr)=0.022/0.022$). These findings suggest that the dog brain represents what is said and how it is said in a human-analogue, lateralised manner; and integrates lexical and intonational cues from verbal praises in subcortical reward centres, revealing an important pre-linguistic capacity of a non-primate species.

- O10 - WHY DO PEOPLE LIKE SMALL DOGS WITH EXTREME PHENOTYPES? A REPRESENTATIVE STUDY OF DANISH OWNERS OF FOUR DOG BREEDS

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Highlights:
A survey was conducted among owners of four small dog breeds of which three have extreme phenotypes. Motivations for acquiring the dogs, welfare problems and owner-dog relationship were measured. For owners of two of these breeds, health and other breed properties were not important motivators. Owners of breeds with highest levels of welfare problems had closer relationships with their dogs.

Keywords: *acquisition; dog-owner relationship; extreme dog breeds; welfare problems*

Purebred dogs suffer a range of welfare problems due to extreme phenotypes and high levels of inbreeding. Despite this, the popularity of purebred dogs with extreme phenotypes and high disease-load does not seem to be declining. Based on a representative study of owners of three small dog breeds with breed-related health problems (French Bulldog, Chihuahua, and Cavalier King Charles Spaniel), and owners of one relatively healthy dog breed (Cairn Terrier) as a control group, we investigated this seeming paradox in more detail. We examined the motivational factors behind the acquisition of dogs of these breeds, the association between the levels of welfare problems, and the quality of the owner-dog relationship measured by means of the LAPS. A random sample of 750 owners of each of the four selected dog breeds registered with the Danish Dog Register was invited to participate in a survey questionnaire. Of the 3000 randomly drawn owners (4x750), there were current addresses on 2636. 896 of these owners responded to the questionnaire giving a response rate of 34%. One main result is that there were clear differences with respect to the importance of breed characteristics, such as health, when acquiring a dog ($F(3, 818) = 26.9$, $p < 0.001$) where owners of Chihuahuas and French Bulldogs were less motivated by this. Also, higher levels of welfare problems were positively correlated with a closer owner-dog relationship. This indicates that information about breed specific welfare problems will only have a limited impact on the demand for dog breeds with extreme phenotypes.

- O11 - FELLOW HUMAN? FELLOW DOG? PET DOGS' RELATIONSHIPS WITH THEIR OWNER AND WITH DOGS LIVING IN THE SAME HOUSEHOLD

G. Cimarelli[1],[2],[3]* (presenting), S. Marshall-Pescini[1],[2], F. Range[1],[2], Z. Virányi[1],[2]

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Highlights:

We compared pet dogs' relationships with their owners and with dogs living in the same household. We used a newly developed set of tasks to test various aspects of these relationships. Dogs looked more at their owners but synchronized their movements more with their fellow dogs.

Keywords: *dependence; dog-dog relationship; dog-owner relationship; social referencing; social support*

It has been suggested that dogs have evolved a preference for human companionship. At the same time, free-ranging dogs tend to form social groups. Moreover, the relationship of pet dogs with their owners is influenced by the presence of another dog in the same household. To investigate if owners and fellow dogs have the same or different roles for a pet dog, we developed a test battery in which various aspects of the dogs' relationship (dependence, social support, social referencing, etc.) with both the conspecific and human partner are assessed. We tested 65 dogs with their owner and 57 with their conspecific partner that has been living in the same household for at least 12 months. Each dyad was tested in an outdoor area in 5 tasks (exploration, separation, reunion, novel object and social "scary" tests), and the same behaviors of the dogs were coded with both kinds of partners (orientation to partner, synchronization, play, greeting, contact seeking, stress signals, etc.). Preliminary results show that during exploration, dogs look more at their owners (Mann-Whitney U test, $U(113) = 1125$, $p = 0.003$) but that they synchronize their movements more with their conspecific partners (Mann-Whitney U test, $U(113) = 2532$, $p < 0.001$). These findings suggest a differential role of the owner and of a conspecific partner in the social life of a pet dog that might use the owner as a source of information and consider a fellow dog more as a companion to share activities with.

- O12 - THE EFFECTS OF SEX AND GONADECTOMY ON A SPATIAL NAVIGATION TASK IN DOGS

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Highlights:

Sex differences and the effect of gonadectomy in spatial skills are poorly documented in dogs. 64 dogs underwent a T-maze task consisting of learning, memory and reversal-learning tests. Intact females showed better performance than intact males and ovariectomized females. Sex and gonadectomy have effects on spatial navigation task in dogs.

Keywords: *dog; gonadectomy; maze; sex differences; spatial task*

Sex differences in spatial cognition have been demonstrated in many mammal species, but not widely studied in dogs. Sixty-four pet dogs divided in four equally sized groups (intact males, orchiectomized males, intact females, ovariectomized females) were tested in a T-maze task consisting of three stages. In the first learning test, dogs had to learn which of the two arms led out of the maze. After 2 weeks, memory was assessed. In the last, reversal-learning test, the correct exit arm was inverted compared to the learning test.
The whole task was successfully completed by 81.3% of intact and 56.3% ovariectomized females, 62.5% of intact and 50% of orchiectomized males. Intact females made fewer errors than intact males in the learning and memory tests (adjusted $P<0.05$, t-test) and chose with a lower latency in trials of the reversal-learning test (adjusted $P<0.05$, GLMM). The effect of gonadectomy was separately assessed within each sex. Intact females made fewer errors in learning and memory tests (adjusted $P<0.05$) and chose with a lower latency in trials of the reversal-learning test (adjusted $P<0.05$) than ovariectomized females. Intact males showed higher latency than orchiectomized males in reversal-learning test ($P<0.05$).
Results show clear sex-related differences in spatial cognition. Gonadectomy mainly affected females, inducing a general worsening of performance in ovariectomized subjects. Findings underline the role of sex on spatial cognition in dogs, which may be relevant for specific training where good navigation skills are required. Results also raise questions about the possible consequences of gonadectomy on dog's cognitive abilities.

- O13 - RISK FACTORS ASSOCIATED WITH HUMAN DIRECTED AGGRESSIVE BEHAVIOR AND DOG BITES

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Highlights:

Two online surveys of dog owners were used to investigate human directed aggressive behavior. Multivariate analyses showed 'problem' and 'biting' dog ownership could be correctly predicted. The resulting predictive models include dog, owner and environmental risk factors.

Keywords: *aggressive behaviour; dog bites; dogs; risk factors*

Human directed aggressive behavior (HDAB), as an international public health issue and welfare concern, has been subject to various studies that aim to identify associated risk factors. These studies often use biased samples, fail to incorporate a control population, and are narrowly focussed on the identification of dog-specific risk factors to predict only high severity HDABs such as biting. The current study used a holistic approach to investigate both dog and non-dog factors in terms of association with HDAB. An online survey was conducted to collect data from owners of self-identified 'problem' or 'non problem' dogs in 2014and 2015. Binary logistic regression was used to model the effect of variables upon 'problem' dog ownership in both samples. In 2014 (n=865), the model incorporated 19 predictive factors and correctly predicted 78.2% of cases (Omnibus $X2(29) = 162.457$, $p < .001$). Between 22.0% and 31.8% of variability was explained. Similarly, the model applied to the 2015 sample (n=1941) correctly predicted 77.9% of cases (Omnibus $X2(32) = 773.017$, $p < .001$). Between 32.9% and 44.1% of variability was explained, again using 19 predictive factors. Further analysis showed that 'biting' dog ownership could be correctly predicted from samples of 'problem' dog owners (results in presentation). The analyses of both samples represent a substantial improvement upon previous attempts to predict HDAB, with implications for dog bite prevention and management of HDAB. The results also indicate a significant difference between dogs that display biting behavior, and those that display other HDAB.

- O14 - LOOKING BACK: A BYPRODUCT OF 'GIVING UP' OR A MEASURE OF 'HUMAN-DIRECTED COMMUNICATION'? RE-EVALUATING THE UNSOLVABLE TASK PARADIGM WITH WOLVES, PACK DOGS, FREE-RANGING DOGS AND PETS.

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Highlights:

Looking back at humans during was compared in wolves, equally raised dogs, free-ranging and pet dogs. When controlling for persistence the wolf-dog difference mostly disappeared. Where differences remained they appeared due to socialization levels.

Keywords: *looking back; persistence; wolf-dog differences*

'Looking back' at humans, when confronted with an unexpectedly unsolvable task, has emerged as one of the major wolf-dog differences (Miklosi et al., 2003) suggesting that dogs have evolved such skills to adapt to the human environment. However, wolves are more persistent than dogs in independent problem solving tasks (Frank & Frank, 1985; Udell, 2011) and looking back later may simply be a consequence of 'giving up' later. Here we compared 'looking back' at humans in free-ranging (n=21), pet (n=20), captive pack living (n=20) dogs and wolves (N=15) in the unsolvable task paradigm, whilst controlling for persistence (i.e. time spent manipulating the apparatus). Results showed that persistence affects 'looking back' in that no differences between wolves and (all groups of) dogs emerged in the latency to look back when this variable was controlled for (LM: $F=0.71$, $p=0.55$ without controlling for persistence $F=26.52$, $p<0.0001$). Furthermore, wolves interacted more with the apparatus than all dog groups (all $p<0.002$), whereas no differences in persistence emerged between dog groups. Controlling for persistence, pet dogs looked for longer than free-ranging dogs and wolves (both $p<0.01$) but not pack dogs. Wolves did not differ from free-ranging and similar raised and kept pack dogs. Taken together results suggest an effect of socialization rather than species on looking back behavior.

References

Frank, H., Frank, M.G., 1985. Comparative manipulation test performance in 10-week-old wolves (*Canis lupus*) and Alaskan Malamutes (*Canis familiaris*) – a Piagetian interpretation. J Comp Psychol 99, 266–274.

Miklósi, A., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., Csányi, V., 2003. A simple reason for a big difference wolves do not look back at humans, but dogs do. Curr Biol 13, 763–766.

Udell, M.A.R., 2015. When dogs look back: inhibition of independent problem-solving behaviour in domestic dogs (*Canis lupus familiaris*) compared with wolves (*Canis lupus*). Biol Lett 20150489.

- O15 - NON-LINEAR PHENOMENA IN DOG WHINES AS POTENTIAL INDICATORS OF SEPARATION ANXIETY

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Highlights:

Our aim was to explore the communicative function of non-linear phenomena in dog whines. We assumed that the occurrence on non-linear phenomena is related with elevated levels of stress. Whines of dogs with Separation-related anxiety carried nonlinear phenomena more often. This suggests that the presence of non-linear phenomena indicates higher level of stress in dogs.

Keywords: *dog; nonlinear phenomena; separation-related anxiety; vocal communication*

Although nonlinear phenomena (sudden changes in frequency, NLP) are often present in healthy vocalizations, their communicative functions are unclear. Fitch et al., (2002) 'unpredictability hypothesis' was tested in several species providing support for their attention-evoking function, while Blumstein & Récapet, (2009) suggested that nonlinearities can act as honest stress level indicators. We suggest that dog whines, often carrying NLPs, provide an excellent model to study this, with comparing whines from dogs experiencing different stress level during separation from their owner. Moreover, Separation-related Anxiety is one of the most common behavioral problems among dogs, thus there is a great importance to find novel diagnostic tools. In this study, we aimed to explore the possibility of the role of NLPs in stress level communication. Using separation and vocal behavior questionnaires, we recruited 70 family dogs that whine during separation, and according their owners have or lack separation-related anxiety. During 3 minute separation in the lab, we recorded their whines and measured the occurrence of NLPs. We compared the number of nonlinear elements between subjects reported to have separation-related problems and healthy ones. We found significantly more nonlinear phenomena in the whines of the subjects with higher anxiety level (Binomial GzLM: χ^2=4.209, p=0.04). Additionally we are currently running quantitative acoustical analysis to find associations between the inner state of the subjects and other acoustical parameters of their whines. Our preliminary results are promising, suggesting that nonlinear phenomena in whines are possibly act as indicators of stress level in dogs.

References

Blumstein, D.T., Récapet, C., 2009. The Sound of Arousal: The Addition of Novel Non-linearities Increases Responsiveness in Marmot Alarm Calls. Ethology 115, 1074–1081.

Fitch, W.T., Neubauer, J., Herzel, H., 2002. Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. Anim Behav 63, 407–418.

- O16 - UNDERSTANDING DOG-DOG INTERACTIONS: IF EXPERIENCE DOESN'T COUNT, WHAT DOES?

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Highlights:

This study compared the accuracy of interpretation between individuals with differing levels of experience with dogs. Statistical analysis revealed that experience level did not affect the total number of accurately identified behaviours. Binary logistic regression (BLR) found significant associations with the body and facial cues used by respondents who correctly identified a dog's behaviour.

Keywords: *behaviour; dog interactions; experience; video test*

Respondents (n=1380) were recruited using online forums and discussion groups. They were asked to view four videos of dog-dog interactions and choose the single descriptor that most closely described each dog's behaviour in each video (confident, submissive, fearful, playful or aggressive). Respondents were asked which facial and body cues they had focussed on when making their decision. Appropriate statistical contrasts were used to compare experience groups (ranging from qualified vet to no experience with dogs), and BLR was used to identify facial and body cues associated with correct identification of a dog's behaviour. The proportion of correct behaviour identifications ranged from 23.0% (aggression) to 77.8% (playful), with 34.1% of respondents incorrectly identifying aggressive behaviour as playful. People with more experience with dogs did not achieve a significantly larger total number of correct answers ($p = 0.2418$, KW statistic 9.153). BLR models found significant associations between respondent-observed behaviours and the likelihood of a correct answer. For example, respondents who noticed the play-bow or play-face were more likely to correctly identify play behaviour, and those noticing raised hackles or showing teeth correctly identified aggression. Self-reported level of experience with dogs did not influence performance in the video observation test, indicating that experience alone may not be an indicator of competence in interpreting dog behaviour. Successful identification was linked to observation of specific facial and postural signs, which suggests that education should focus on teaching people to attend to those features.

- O17 - AGING OF ATTENTIVENESS IN PET DOGS: DOES TRAINING MAKE A DIFFERENCE?

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Highlights:

We tested aging of attentiveness to an object and a human in 183 pet dogs over 6 years. Sustained attention declined with age but selective attention remained intact. Prior results of aging in Border collies were generalizable to a mix of pet dogs. Lifelong training influenced different measures of attentiveness.

Keywords: *aging; attention; pet dogs; training*

Aging of attentiveness affects cognitive functions like perception and working memory, which can seriously impact communication between dogs and humans, potentially hindering training and cooperation. In previous studies, aged laboratory beagles and pet border collies showed decline in selective attention ability (Snigdha et al., 2012; Wallis et al., 2014). However, much less is known about aging of attentiveness in pet dogs in general rather than specific breeds. Using 183 pet dogs (75 Border collies and 108 other breeds) divided into three age groups (late adulthood (>6-8yr), senior (>8-10yr) and geriatric (>10yr)), we assessed progress of aging of sustained and selective attention in older dogs and evaluated influence of training as well as explored if prior results in border collies are generalizable. Dogs were tested in two tasks; first, measuring sustained attention towards the stimuli (toy and human); second, measuring selective attention towards the experimenter by means of clicker training for eye contact. There were significant effects of age ($F(1,173.20)=29.70$, $p<0.001$) but no effect of training ($F(1,168.02)=2.86$, $p=0.09$) on latency to orient to the stimuli. Duration of looking decreased with age ($F(1,179.13)=16.64$, $p<0.001$) and increased with training ($F(1,178.19)=10.92$, $p<0.01$). Dogs' latency to eye contact decreased with training ($F(1,180)=14.92$, $p<0.001$) whereas age had no effect ($F(1,180) =0.38$, $p=0.530$). Border collies did not differ from other dogs in any measures of attention. In conclusion, aged dogs showed decline in sustained attention whereas selective attention remained intact, demonstrating that these tests are suitable to detect aging of attentiveness in older pet dogs. Importantly, training seemed to hinder the aging of attentiveness.

References

Snigdha, S., Christie, L.A., De Rivera, C., Araujo, J.A., Milgram, N.W., Cotman, C.W., 2012. Age and distraction are determinants of performance on a novel visual search task in aged Beagle dogs. Age 34, 67–73.

Wallis, L.J., Range, F., Müller, C.A., Serisier, S., Huber, L., Virányi, Z., 2014. Life span development of attentiveness in domestic dogs: drawing parallels with humans. Frontiers in psychology 5, 71.

- O18 - COMPARISON OF EFFECTS OF COMPANION DOGS AND SERVICE DOGS ON QUALITY OF LIFE IN PEOPLE WITH MOVEMENT DISORDERS

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Highlights:

A comparison of effects of companion dogs and service dogs on quality of life in people with movement disorders. Participants with diagnosed movement disorders and either companion or service dogs were followed for 12 months. Service dogs seemed to offer more avenues to enrich quality of life but the service dog model does not suit everyone. An expanded perspective of the service dog concept was suggested with implications for service dog organizations.

Keywords: *companion dogs; movement disorders; quality of life; service dogs*

Previous studies have focused on the impact of either companion dogs or service dogs on human health and well-being. A need remains to understand comparative effects of companion dogs and service dogs as QOL interventions. Recognising time as a key component in living with chronic conditions and dogs, a longitudinal, predominantly qualitative, case-oriented study design was implemented. Participants with diagnosed movement disorders were prospectively followed for 12 months. Two groups were purposefully recruited; one group (n=7) partnered with, or waited for, Mobility Dogs; a second group (n=10) lived with companion dogs. Interactions with participants at baseline, six and 12 months triangulated data from: semi-structured and walk-along interviews; observations; a photovoice assignment; and a standardised measure of QOL. General inductive analysis of these data indicated eight roles that dogs can play to impact QOL: companion, protector, icebreaker, caregiver, empowerer, motivator, entertainer and tool/assistive technology. Dogs appeared to be a complex QOL intervention fulfilling these different roles, for different people, across different environments. Overall, Mobility Dogs seemed to offer more avenues to enrich QOL but the service dog model does not suit everyone; companion dogs may be equally effective for some people. An expanded perspective of the service dog concept was suggested which has prompted the MADT to reassess and refine aspects of its practice including: increased recognition of psychosocial benefits as a primary reason to apply for a service dog; introduction of smaller dog breeds in addition to the standard retrievers; and provision of more post-placement support to Mobility Dog teams.

- O19 - COMPARING INCIDENCE AND IMPACT OF HEALTH AND BEHAVIOR ISSUES IN AN AGEING POPULATION OF WORKING GUIDE DOGS

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Highlights:

We evaluated health and behavior reasons for removal from service in 8,996 working guide dogs. 13.5% of dogs were removed from service for health reasons and 14.5 for behavior reasons. Of the four main reasons for removal, one was for health and three were for behavior. GSDs work less due to health whilst F2 crossbreeds work less due to behavior.

Keywords: *ageing; breed; epidemiology; guide dogs; heterosis*

Using an existing historical dataset we aimed to identify which health and behavioral factors most impact upon working longevity in a population of qualified guide dogs. A secondary objective was to investigate the influence of breed, crossbreed and age upon emergence of the factors evaluated. The dataset contained all UK guide dogs that ended their service between the years of 1994-2013 (8,996 dogs). Dogs were classified as retired, removed from service for health reasons or behavior reasons. Health removals were broken into 14 categories, according to disease type (Caron-Lormier et al., 2016), whilst behavioral removals were grouped into 10 categories based on factor analysis. Generalized linear models were applied, considering incidence of removals within each category, and the length of working life, comparing against dogs that retired. 72% of dogs reached retirement, whilst 13.5% were removed from service for health reasons and 14.5% for behavior reasons. Retired dogs worked for at least 8.5 years, excepting German shepherd dogs, which had a reduced working life. The main reasons for removal from service were musculoskeletal conditions (n=387), Environmental Anxiety (n=321), Willingness/Confidence (n=311), and Fear/Aggression (n=226). Crossbred dogs were less likely to be removed from service for health reasons. However, F2 crossbreeds were 40% less likely to reach retirement due to behavioral issues. These studies highlight the potential for use of existing data from working dog organizations for understanding health-related ageing, the emergence of behavioral issues over time and the relative effect upon these for different breeds, and crossbreeds.

References

Caron-Lormier, G., England, G.C.W., Green, M.J., Asher, L., 2016. Using the incidence and impact of health conditions in guide dogs to investigate healthy ageing in working dogs. Vet J 207, 124–130.

- O20 - INDIRECT RECIPROCITY IN WORKING DOGS

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Highlights:

Dogs differentiate between cooperators and non-cooperators in an iterated prisoner's dilemma game. Dogs apply decision rules denoting indirect reciprocity. Except for rats, this is the 1th experimental evidence for indirect reciprocity in non-human animals.

Keywords: *cognition; cooperation; indirect reciprocity; working dogs*

Domestic dogs are highly social animals renowned for their advanced cognitive abilities (Ostojic & Clayton, 2014; Fugazza & Miklosi, 2014), even if they may use simple mechanisms in social learning tasks (Mersmann et al., 2011). Previous experiments have shown that they differentiate between cooperators and non-cooperators in an iterated prisoner's dilemma game (Rieder, 2013). Here we tested whether dogs cooperate by indirect reciprocity in a situation where they can pull a rope to provide food for a social partner which they have previously observed to interact with a stooge. Thirteen dogs of the Swiss army were trained individually to pull food for a social partner. In the experience phase, all dogs observed an interaction between either a cooperator or a non-cooperator with a prospective receiver. In the test phase, the focal dogs had the opportunity to provide food either for the previous cooperator or the previous non-cooperator.
Our results show that as predicted, experimental subjects pulled more often for former cooperators than for former non-cooperators ($V = 80.5$, $p = 0.016$). Obviously, dogs recognize the cooperation propensity of social partners just by observing them interact, and they reward cooperators whereas they do not help non-cooperators. Apart from a similar study in Norway rats, this is the first experimental evidence for indirect reciprocity displayed among conspecifics in non-human animals.

References

Fugazza, C., Miklosi, A., 2014. Deferred imitation and declarative memory in domestic dogs. Anim Cogn 17, 237-247.

Mersmann, D., Tomasello, M., Call, J., Kaminski, J., Taborsky, M., 2011. Simple mechanisms can explain social learning in domestic dogs (*Canis familiaris*). Ethol 117, 675-690.

Ostojic, L., Clayton, N.S., 2014. Behavioural coordination of dogs in a cooperative problem-solving task with a conspecific and a human partner. Anim Cogn 17, 445-459.

Rieder, N., 2013. Dogs cooperate with conspecifics by generalised reciprocity. Master Thesis.

- O21 - PUPPY AND ADULT DOG PERSONALITY

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Highlights:

Sevenhundred puppies have been tested using a newly developed puppy test. Using a factor analysis three factors were identified: Biting intensity, Sociality & curiosity and finally Play and collaboration. The dogs were retested using the DMA at 1.5 years of age. Biting intensity and chase correlated as well as the overall activity of the puppy with the aggression of the adult dog.

Keywords: *personality; puppy test; temperament;*

Puppytests have been developed previously, however few if any scientific studies have succeeded in finding a correlation between the behaviour of the puppy and that of an adult dog growing up in a family. The current personality assessment for puppies (”mentalbeskrivning valp” - MV) has been developed in collaboration with SBKs and is constructed using the same principles as for the Dog Mentality Assessment, but with less emphasis on fear. The test takes 15 min/puppy and is done at eight weeks of age. Sevenhundred puppies have been tested so far and three personality factors have been identified: Biting intensity, Sociality & curiosity and finally Play and collaboration. Adult dogs were assessed with the DMA 1.5 years later (N=196), this revealed a significant correlation between Biting intensity in the puppy test and chase from the DMA ($R_s=0.14$, $p<0.03$). The overall aggression of the adult dog was also correlated to the confidence of the puppy as assessed by the test leader ($R_s=0.20$, $p<0.01$). The current puppy test is being implementd and will be used for three years in Sweden before a final evaluation.

- O22 - SIMILARITIES AND DIFFERENCES BETWEEN DOG- AND INFANT-DIRECTED SPEECH

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Highlights:

Infant, dog and adult directed speech were recorded from adult male and female participants. Striking similarities were found between the acoustic features of infant directed and dog directed speech samples. Motherese and doggerel have context- and sex-dependent features.

Keywords: *dog-human communication; doggerel; motherese*

There is growing evidence that pet talk (or doggerel) and infant directed speech (or motherese) have similar acoustic characteristics such as high-pitch register, repetitiveness, and attention-getting devices, however it is still unclear whether doggerel and motherese have gender, age or context dependent acoustic and/or linguistic features. In the present study we collected infant directed (ID), dog directed (DD) and adult directed (AD) speech samples in four different contexts (getting attention, easy task, teaching and predetermined speech situations) from parents whose infants were 0-30 months old and who also had dog at home (N=18 males, 21 females). We hypothesized that AD signals will be markedly different from ID and DD signals, while only minor differences are expected between the latter two. Our results supported our assumptions as we found higher fundamental frequency (F0) in both female and male participants during ID and DD speech compared to AD signals independently from the context (females: $F_{2,17010}$=340.04 , p<0.001; males: $F_{2,12202}$=533.31 , p<0.001). However DD speech was characterized by higher F0 range compared to AD speech only in females ($F_{2,17010}$=9.38 , p<0.01) as males used the same F0 range toward dogs and adults. Last but not least, we found evidence that acoustic features of the ID speech toward 19-30 months-olds resemble most to the DD speech.

- O23 - TRACKING OF WILD WOLVES USING PASSIVE ACOUSTIC MONITORING

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Highlights:

We developed a system for pinpointing the location of wild wolves using their howl vocalizations. Multiple recording devices measure the time difference of arrival of howls. The system has been collecting data in Yellowstone National Park over an entire season. The precision of localization also allows us to distinguish between chorus and cohesion howls.

Keywords: *communication; howling; monitoring; wolves*

Finding and tracking wolves in the wild is an essential element of population conservation and management, and for wolf behavior research. However, wild wolves range widely and avoid proximity to humans, so radio collaring wolves is difficult and expensive. Wolf howling can be detected over distances of 10 kilometers or more, and so can form a potential indicator of the location of the pack. Passive acoustic monitoring (finding the location of the sound source by using the difference in arrival times of the sound at multiple detectors) has been applied successfully for marine mammals and a similar technique could be used for detecting howling wolf packs, although sound propagation in air is much more problematic than in water. We developed a system based on passive acoustic monitoring to identify the location of a vocalizing wolf, based on the time difference of arrival of a howl at multiple autonomous recording devices, synchronized with GPS clocks. We deployed multiple units in Yellowstone National Park over the winter of 2015-2016 and recorded continuously for four months. We demonstrated that it is possible to localize the sound source with good precision, and it is possible to distinguish instances where all the vocalizing animals are together (chorus howling) and when animals are howling in sequence with animals at another location (putative cohesion howls). This technique can be applied both to conservation ends such as population monitoring, and also for research goals such as understanding the nature and role of different types of howling in wolves.

- O24 - THE SOCIAL BEHAVIOR OF NEUTERED MALE DOGS COMPARED TO INTACT DOGS (Canis Lupus Familiaris). VIDEO ANALYSES, QUESTIONNAIRES AND CASE STUDIES

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Highlights:

A combined approach (personality questionnaires, video recordings, case studies) was used to assess the effect of neutering on social behavior of male dogs. Significant differences were found in several behavioral patterns (aggression, fear, molesting other dogs, smelling the genital area, chin rest or behavior indicating high status), emotional reaction to stressful situations and frequency of aggressiveness and fear. Results indicate a negative impact of castration on the social behavior of male dogs.

Keywords: *case studies; male dogs; neutering; questionnaire study; social behavior; video recordings*

Gonadectomy is a regularly performed procedure in domestic dogs. Apart from preventing reproduction, neutering is also conducted for reasons of health and to change or remove undesirable behavior. From the ethological perspective, castration may have a negative impact on the social behavior of male dogs. Using video recordings from Germany and Switzerland of six groups of dogs, consisting of 17 intact and 16 neutered males in total, the social behavior of the dogs was analyzed. Specific behaviors were compared between the castrated and intact males and statistically analyzed. Significant differences were found in patterns of behavior such as smelling and licking the genital area, molesting other dogs, tooth chatter and chin rest (Mann-Whitney-U-Test, $U=419.5$, $p=0.003$). Also the non-castrated males show more behavior indicating high status.
Furthermore, 29 questionnaires based on Turcsán et al., (2011) were completed by the owners and, together with 104 by other dog owners have been incorporated into this study. Here, the results indicate a trend that neutered males react emotionally more instable in stressful situations. Additionally, 54 case studies from our consultancy were evaluated. These show a tendency for aggressive behavior and fear to be more frequent in castrated dogs. The results support data from other studies (e.g. Zink et al., 2014) that castration may have a negative influence on the behavior of male dogs. Neutered dogs may gain attractiveness for intact dogs which can lead to a high stress factor for the castrates. Accordingly dog owners should be aware of the consequences for the dog.

References

Turcsán, B., Kubinyi, E., Miklósi, Á., 2011. Trainability and boldness traits differ between dog breed clusters based on conventional breed categories and genetic relatedness. Appl Anim Behav Sci 132, 61-70.

Zink, C., Farhoody, P., Elser, S., Ruffini, L.D., Gibbons, T.A., Rieger, R.H., 2014. Evaluation of the risk and age of onset of cancer and behavioral disorders in gonadectomized Vizslas. Journal of the American Veterinary Medical Association 244(3), 309-319.

- O25 - INHIBITORY CONTROL IN DOGS: WHAT ARE WE ACTUALLY MEASURING?

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Highlights:

We tested 67 dogs in an inhibitory control test battery, consisting of five tasks. Results show that dogs' behavior in the different tests was not correlated. Thus indicating that inhibitory control is strongly context specific in dogs.

Keywords: *context specificity; dogs; inhibitory control; test battery*

Inhibitory control, i.e. the ability to refrain from an immediate response in favor of a more advantageous behavior, is an important basis for more complex behaviors, such as cooperation. Although, a variety of different tests have been used to study inhibitory control in different species, only few studies investigated whether the individuals' behavior is consistent across tasks. We tested 67 dogs in a test battery, consisting of five non-social tasks all aimed at measuring inhibitory control. Four tasks (i.e. delay of gratification, reversal learning, detour reaching and middle cup task) have been frequently used in the animal literature, whereas the fifth task was designed as a combination of the other four tasks where dogs were required to perform an action away from a food reward in order to obtain it. Although we found great variability within tests, results revealed that they were not correlated with each other (Spearman rank correlation: $r_s < 0.23$). Thus raising the question of what the tasks are actually measuring and whether inhibitory control is essentially quantifiable in an experimental context. Future studies are needed to disentangle the different components of inhibitory control for gaining a complete understanding of this strongly context-specific ability and how it might influence more complex behaviors.

- O26 - OWNER INTERACTION STYLE AFFECTS DOG PHYSIOLOGY DURING A STAGED THREAT

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Highlights:

Heart rate variability after a staged threat was higher when the owner was present, than when the dog was alone. Dogs with owners with a friendly interaction style had lower HR. We therefore suggest that owners can be effective emotional social supporters of their dogs.

Keywords: *dog stress coping; interaction style; owner-dog relationship*

Human – dog dyads engage in a mutual social relationship, potentially resulting in physiological effects such as heart rate (HR) and heart rate variability (HRV, a measure of "relaxation") in both partners. We tested 132 owner-dog dyads to investigate our hypothesis that HR and HRV in dogs are related to owner interaction style. Owners were18 to 60 years of age, their intact dogs (i.e. not neutered or spayed) were 1.5 to 8 years. Dyads were tested during and after a mild experimental threat situation. HR and HRV were measured from owners and dogs by using HR monitoring belts (Polar-RS800CX). Behavior was coded via the Noldus Observer XT10 ®. Median HR was higher during the threat than after, for owners and for dogs (Wilcoxon: n=107, T=-8.737, p<0.001 and n=115, Z=-9.133, p=<0.001). Dog HRV was higher after the threat with the owner present than without the owner present (Wilcoxon: n=106, Z=-2.971, p=0.003). Based on HR parameters we found two major clusters for dogs. Cluster 2 dogs (low HR and high HRV) had more friendly owners (MWU: n=104, z=-1.961, p=0.049), with whom dogs were more behaviorally synchronized (MWU: n=105, Z=-3.817, p<0.001) and showed more friendly behavior towards the threatening person during the threat with and without than those from cluster 1 (MWU: n=104, Z=-2.859, p=0.004; n=105, Z=-3.840, p<0.001). Our results indicate that owner interaction style is reflected by dog behavior and physiology; friendly owners tend to have secure, friendly and relaxed dogs. The research was funded by the Austrian Science Fund (FWF): P23345 B17.

- O27 - WHAT DOES MY DOG UNDERSTAND ABOUT ME?

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Highlights:

Three different groups of dogs were exposed to two emotional situations and one control situation. Behaviors, heart rate and heart rate variability data were collected. Behavioral reactions towards owner varied differently in the proposed situations.

Keywords: *dog-owner relationship; emotional recognition; heart rate variability*

Dogs and humans have shared a long part of their history together and dogs were intensively selected for many different purposes. In dogs, the domestication process may have resulted in advanced socio-cognitive abilities and strong predisposition to form affectional bonds (Hare et al., 2002). This have led to an experimental protocol to investigate emotional contagion in domestic dogs (Custance & Mayer, 2012). Results showed as dogs oriented toward their owner or a stranger more often when the person was pretending to cry than when they were talking or humming. Our study expands the previous work, analyzing behavioral and cardiac reactions of three different groups of dogs when their owners are crying, laughing, or emitting an unusual but emotively neutral sound "Om". Behaviors and cardiac data were collected during the baseline, the stimulation and immediately after it. "Om" induced only an attentive state in dogs because, likely, this is due to the sound being very unusual (increase in Attention: χ=6.000, P=0.050). Laughing is a very common thing for humans and dogs are quite accustomed to being exposed a laughing human, therefore dogs were simply waked up if they were resting (decrement in Rest: χ=7.312, P=0.026). Crying elicited a wide range of different physical interactions between dogs and owners (χ=6.857, P=0.032); besides, animals actively sought the owner, approaching them (χ=6.831, P=0.041). This may suggest that dogs could have linked crying with an unpleasant situation. Cardiac data are currently being analyzed.

References

Custance, D., Mayer, J., 2012. Empathic-like responding by domestic dogs (*Canis familiaris*) to distress in humans: An exploratory study. Anim Cogn 15, 851-859.

Hare, B., Brown, M., Williamson, C., Tomasello, M., 2002. The domestication of social cognition in dogs. Science 298, 1634-1636.

- O28 - BREED DIFFERENCES IN DOG BEHAVIOR CO-VARY WITH GENETIC RELATIONSHIPS BETWEEN BREEDS

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Highlights:

We assessed the extent to which breed differences in dog behavior are associated with the genetic relationships between breeds. Using behavioral data from the Canine Behavioral Assessment and Research Questionnaire, and a molecular neighbor-joining tree of modern dog breeds, we quantified phylogenetic signal – the extent to which closely related breeds exhibit similar trait values. Most behavioral traits showed strong phylogenetic signal suggesting that evolutionary history can account for the covariance of behavioral traits across breeds.

Keywords: *behavior; dog; evolution; phylogeny; systematics*

Molecular phylogenetic approaches have led to major refinements in our understanding of the genetic relationships between dog breeds. These advances create rich opportunities to examine how breed differences in cognitive and behavioral traits relate to the history of breed diversification. Phylogenetic signal is a statistical measure of how trait variation correlates with the relatedness of species in a phylogeny and is often an important first step in comparative analyses. We assessed phylogenetic signal in behavioral traits measured with the Canine Behavioral Assessment and Research Questionnaire (C-BARQ; > 16k individuals) analyzed in conjunction with a molecular neighbor-joining tree for modern dog breeds. In this sample of >50 breeds, the majority of traits exhibited strong phylogenetic signal (Blomberg's Kappa, $p < 0.01$) suggesting that the evolutionary history of breeds can account for covariance in behavioral traits. In addition to a general pattern of trait similarity among closely related breeds, our analyses also reveal evolutionary convergences across the dog phylogeny, as well as cases in which individual breeds are highly derived relative to close genetic relatives. Collectively these data provide a critical first step in linking breed differences in behavior to the patterns of diversification in dog evolution, and set the stage for future research aimed at uncovering the molecular underpinnings of behavioral differences between breeds.

- O29 - DIETARY STUDY OF FREE-RANGING DOGS IN RURAL ZIMBABWE

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Highlights:

Food intakes and feeding behaviors were quantified in 16 radio-collared, free-ranging dogs. Anthropogenic resources accounted for 87.5% of the diet, mostly independently scavenged. The most frequently eaten item was sadza (maize-meal porridge) followed by human feces. Human feces was more consistently available than carrion and of higher protein content than sadza.

Keywords: *carrion; diet; feeding behavior; free-ranging dogs; human feces*

While the importance of human-derived food in the maintenance of free-ranging domestic dog populations is acknowledged, little attention has been paid to the role of human feces as human-derived food. This may be important in less developed regions where basic sanitation is lacking, and risks to human health and wildlife conservation from uncontrolled dog populations are high. In this study of free-ranging dogs in a remote area of rural Zimbabwe, direct observations of 16 focal animals radio-tracked over 18 months indicated that the most important components of their diet, by volume, were mammalian carrion (49%), sadza (22%) and human feces (21%). Whilst it was not practical to accurately measure the nutrient composition of mammalian carrion, chemical analysis was conducted on the sadza and human feces that accounted for 43% of the total dietary intake. Human feces had a relatively high nutritional value, contributing 10.0g crude protein (CP) per 100kJ compared with 4.5g CP per 100kJ for sadza. It has been suggested that cleaning up human wastes may have played a pivotal role in the domestication of the dog and yet the contribution of human feces to the diets and behavioral ecology of contemporary free-roaming dogs is given little recognition.

- O30 - OWNER ADULT ATTACHMENT STYLE AND THE RESPONSES OF DOGS TO CHALLENGING SITUATIONS

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Highlights:

The aim of this study was investigate relationship styles between dogs and owners. Owner adult attachment style was measured using a questionnaire. Dog-owner dyads were tested in four challenging events and in a separation and reunion test. Owner adult attachment style influenced dog behavior during the tests and may reflect their caregiving towards dogs.

Keywords: *attachment style; behaviour; dog-owner interaction; dog-owner relationship; dog welfare*

A person's AAS describes how they perceive their relationship to other people, but may also reflect their caregiving behavior. In this study, we measured the AAS of 51 owners of Golden retrievers, using the Adult Attachment Style Questionnaire (ASQ). Also, we observed the dog-owner dyads during four challenging events. These included two different sudden surprises (visual (V) and auditory (A)) and two tests where a strange-looking person approached the dyad (AP). In the separation and reunion test, the dog was left alone for three min and its behavior observed. The interactions between dog and owner were observed before and after separation. Spearman rank correlation tests showed that the more confident the owner (according to their score in the ASQ), the longer the dog oriented to the sudden stressors (V:$P=0.01$,$R^2=0.35$; A:$P=0.03$,$R^2=0.30$) and the shorter its latency to approach the visual stressor ($P=0.001$,$R^2=-0.28$). The more ambivalent the owner, the longer the dog oriented to the owner during challenging events (V:$P=0.005$,$R^2=0.38$; AP:$P=0.02$,$R^2=0.33$) and it showed less tail wagging upon reunion ($P=0.04$,$R^2=-0.29$). The more avoidant the owner, the longer the latency for the dog to approach the auditory stressor ($P=0.02$,$R^2=0.34$). These dogs barked more during separation ($P=0.004$,$R^2=0.40$), and such owners initiated more physical contact upon reunion ($P=0.04$,$R^2=0.28$). This implies that dogs may develop different strategies to handle challenging situations, based on the type of support they get from their owner. Moreover, it indicates that a person's caregiving behavior towards their dog is linked to how they relate to other people and interact with them.

- O31 - THE VIDOPET – A RELIABLE AND VALID ASSESSMENT OF PERSONALITY IN PET DOGS

B. Turcsan[1],[2]* (presenting), L. Wallis[1], Z. Virányi[1], F. Range[1], C.A. Müller[1], L. Huber[1], S. Riemer[1],[3]

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Highlights:

A personality test battery was devised and performed on 217 dogs. Principal component analysis on the coded variables yielded five traits. The test showed excellent reliability, good validity and high temporal consistency after >3 years. The VIDOPET (Vienna Dog Personality Test) is a suitable instrument for measuring dog personality.

Keywords: *coding; dog personality test; rating; reliability; validity*

Despite increasing attention on the development and evaluation of instruments assessing dog personality, adequate reliability and validity criteria are still infrequently provided in most studies. To address this lack, and to improve the methodological standardization of dog personality research, the current study aimed to develop a dog personality test and to provide a comprehensive evaluation of its reliability and validity.
The Vienna Dog Personality Test (VIDOPET) consists of 15 situations and was performed on 217 pet dogs. The dogs' behavior during the test was evaluated using both video coding and video rating methods, and the participating owners were also asked to fill in a personality questionnaire about their dogs. The coding data were subjected to a two-step principal component analysis which yielded five traits: Sociability-obedience, Activity-independence, Novelty seeking, Problem orientation and Frustration tolerance. The test location and test person had no significant effect on the dogs' performance. We found excellent inter- and intra-observer reliability, adequate internal consistency, and good temporal consistency in behavior when re-testing a subsample of 37 dogs after an average of 3.8 years. The construct validity of the test was investigated by analyzing the correlations between the results of the video coding, video rating, and the owners' questionnaire assessment. Most of the predicted correlations between these three assessments were significant, although the coefficients were usually low or moderate. These results demonstrate that the VIDOPET is a highly reliable and valid assessment for measuring dog personality.

- O32 - INVESTIGATING THE LINK BETWEEN LATERALITY AND PERSONALITY TRAITS IN DOGS

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Highlights:

We investigated possible associations between lateral behaviour and personality traits in dogs. A paw preference test was used to assess individual lateral bias in pet dogs. Ambilateral and lateralized dogs scored differently on four personality traits. Lateral bias offers a potential novel indicator of personality in dogs

Keywords: *domestic dog; laterality; personality*

Behavioural laterality reflects the divergent processing by each brain hemisphere. According to the laterality–valence hypothesis, left-lateralised individuals (reflecting right hemispheric dominance) are more likely to show fearful and aggressive responses, whereas right-lateralised individuals (reflecting left hemispheric dominance) would be more likely to be calm and explorative. Measures of directionality and strength of laterality have been shown to be associated to emotional stress, problem solving and personality in different vertebrate species. In this study we investigated if lateralised (left or right) and ambilateral animals differed in their behavioural response to a standardised personality test. The dog's preferred paw used to hold a Kong™-ball toy filled with food was scored as a laterality measure. Binomial tests were used to determine distribution of pawedness. The direction and strength of the dogs' paw use was assessed by calculating a handedness index. The Dog Mentality Assessment (DMA) test was used to assess the dogs' personality: six traits (Playfulness, Curiosity/Fearlessness, Chase-proneness, Sociability, Aggressiveness, Distant-playfulness) and a broader Shy-Boldness dimension were extracted and associated to different measures of laterality. Non-parametric tests showed that ambilateral dogs scored significantly higher for the traits of Playfulness ($U=24$, $p=0.005$), Distant-playfulness ($U=28$, $p=0.01$), Curiosity/Fearlessness ($U=38$, $p=0.05$) and the Shy-Boldness dimension ($U=32$, $p=0.02$) than lateralised dogs (independent of direction). No significant differences emerged between left and right biased dogs; however, results suggest that measures of laterality such as strength could be suitable indicators of dog's personality.

Poster Presentations

- P01 - THE DOMESTICATION FROM THE WOLF TO THE DOG IS BASED ON COEVOLUTION. THE EVOLUTIONARY CONTINUITY OF THE BRAIN ENABLED BOTH TO SOCIAL CONTACT AND EMPATHY

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Highlights:

The domestication from the wolf to the dog is based on coevolution. Humans and wolves are highly social mammals living in familiar clans. During Paleolithic period they were living in the same ecological niche, hunting the same big pray as cooperative groups. Due to the evolutionary continuity of the brain both evolved very similar refined social communication, which permits interspecific cooperation.

Keywords: *coevolution; domestication of dogs; epigenetics; pro-social neurotransmitters; stress axis*

Increasing social contact between humans and wolves enhanced empathy between them and started epigenetic modulation of the HPA-stress axis. Our model of the active social domestication considers that domestication is essentially an epigenetic based process of changing the interactions of HPA stress axis and 5-hydroxytryptamine (5-HT) system. Both are closely cross-regulated. Changes in their interactions are of particular relevance when regarding domestication processes of animals.
Operated by epigenetic modulation i.e. social licking and grooming enhance hippocampus Glucocorticoid receptor (hGCR) expression via increased serotonin and subsequently increased NGF levels binding on GRexon1;7promotorbloc. Increased hGCR density inhibits the activity of HPA stress axis. We consider additional nutrition changes like methionin decrease and thryptophan increase during further coevolution to decrease dogs stress reaction via epigenetic modulation.
Neural structures which are important for learning could increase. The domestic wolf became a social dog being able to work together with humans. Hunting and working together promotes the process of reducing stress and increasing pro-social neurotransmitters for each other. This is considered as base of human-dog-bonding and benefit of dog facilitated therapy. We maintain that also human learning and social abilities might have improved.

References

Jung, C., Pörtl, D., 2015. Tierisch beste Freunde: Mensch und Hund - von Streicheln, Stress und Oxytocin. Schattauer-Verlag, Stuttgart Germany.

Pörtl, D., Jung, C., 2014. Die aktive soziale Domestikation des Hundes: Ein neurobiologisch begründetes Modell zur Mensch-Hund-Beziehung. BoD, Norderstedt, Germany.

- P02 - MOVING ON: ANIMAL ETHICS IN THE DOG-HUMAN SOCIETY

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Highlights:

Ethical considerations about dogs as subjects and human responsibilities. Animal ethics as guidance to evolve from welfare to quality of life. Opportunities coming from the study and practical application of animal ethics.

Keywords: *animal ethics; animality; dog-human interaction; quality of life*

In recent years, one of the emerging fields of study in the dog-human interaction has been cognition and the emotional and affiliative side of dogs. The application, however, of this growing insight, does not necessarily lead to a better understanding of dogs as subjects, which arises questions from an ethical perspective.

The study of animal ethics within the dog-human relationship is crucial to develop a critical view on things we still assume to be normal in our coexistence with dogs, a coexistence were the human benefit of the relationship often still prevails. Animal ethics can be considered as compass for decisions, choices and developments, in research and daily applications, to understand dogs as subject.

Key factor within this ethical progress is the focus on integrated quality of life, in which activities between human and dogs can be discussed and questioned from an animal-ethics point of view. Autonomy, integrity, dignity and vulnerability are the coordinates for a more ethical and modern understanding of interactions, allowing a critical, non-anthropocentric perspective, to move away from a consideration of dogs as trainable presence, to dogs as active agents. So dogs can bring a moral and cultural contribution, also for human animals, for a further evolution of coexistence in which both species are equally active contributors.

- P03 - REVERSE CANINE SUSCEPTIBILITY TO THE EBBINGHAUS-TITCHENER ILLUSION

S.-E. Byosiere* (presenting), L.C. Feng, J.K. Woodhead, N.J. Rutter, P.A. Chouinard, T.J. Howell, P.C. Bennett

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Highlights:

Eight dogs were tested on the Ebbinghaus-Titchener and Delboeuf illusions. Dogs showed reversed susceptibility to the Ebbinghaus-Titchener illusion but were not susceptible to the Delboeuf. Ebbinghaus-Titchener reversed susceptibility is best explained by assimilation theory.

Keywords: *Delboeuf; domestic dog; Ebbinghaus-Titchener; geometric illusion; illusory contours; reversed*

Geometrical visual illusions have been tested in a number of non-human species to determine whether or not they are perceptually tricked in the same ways as humans are. However, this has never been tested in the domestic dog (*Canis familiaris*). In this study, a two-choice simultaneous discrimination paradigm was used to teach eight dogs to indicate which of two circles presented on a computer monitor appeared largest. Two circles, either the same size or of different sizes, were then presented embedded in three different displays that, in humans, would result in perception of an illusion. These included the classical display of the Ebbinghaus-Titchener illusion, an illusory contour version of this illusion, and the classical display of the Delboeuf illusion. All eight dogs showed evidence of misperceiving the relative size of the circle stimuli in both Ebbinghaus-Titchener conditions ($p < .0001$, $p < .026$) although, remarkably, in the opposite direction to humans. Results from the Delboeuf illusion were less consistent and not significant as a group ($p > .106$). However, 2 of the 8 dogs also showed statistically significant reversed susceptibility relative to humans. This reversed susceptibility has only previously been reported in pigeons and chickens and is best explained by assimilation theory rather than other visual cognitive theories explaining susceptibility to this illusion in human. Our findings overall appear to reflect higher-order conceptual processing in dogs that cannot be explained by accounts restricted to low-level mechanisms of sensory integration.

- P04 - FACTORS EFFECTING POLICE DOG PERFORMANCE

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Highlights:

540 tests describing the performance of service dogs from the Austrian Police in terms of relation between overall success and age resp. interrelationship of success in different parts of the tests were analyzed. Overall success is not related to age but older dogs perform better in disciplines, which take a lot of self-assurance. General obedience describes best overall success in the police dog tests.

Keywords: *performance; personality; police dog; training*

The dogs of the Austrian Police are generally trained in use of force and searching for objects and persons also. The basic training ends with a test when dogs are at an age of about 2 years. Some of the older dogs are tested during the police dog championship, which takes place every second year and covers the same disciplines. We analyzed the results of these tests (basic training n=396, championship, n=144) in relation to the quality of the dog (age, special training), the quality of the handler (length of service, special training, attachment to the dog) and the interrelationship between the different disciplines. Results of general obedience describe overall results best. Compared to other disciplines general obedience and overall test performance show the highest correlation. Whereas in general obedience the handler is in maximal control over the dog, in searching the dogs have to work self-reliant, making their own decisions. However dogs with high success in obedience perform well in searching too. Overall success of the basic training resp. the championship is not related to age. Certainly in use of force, where it takes a lot of self-confidence from the dog, dogs older than 3 years show a better performance than younger dogs. Attachment of dog and handler as well as special training of both modify these results. It seems that personality of the dog and the handler as well as training methods are the most important factors determining performance of the team.

- P05 - LIVESTOCK GUARDING DOGS (LGDS) IN FINNISH AND ESTONIAN ARCHIPELAGO AND COASTAL AREAS: MULTI-ROLE OF DAMAGE PREVENTION METHODS

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Highlights:

The aim was to analyse the use of LGDs in human-dominated landscape and reintroduction of grey wolf. The longitudinal study focused on experiences in Estonian and Finnish archipelago and coastal area. In Estonia LGDs decreased damages and increased animal welfare - benefits for agritourism observed. In Finland LGDs were more an answer towards the fear of damages and increased feeling of safety.

Keywords: *dog behaviour; human-dominated landscape; livestock guarding dogs; mutualistic system; wolf reintroduction,*

The objective of this longitudinal multicase study was to analyse the use of Livestock Guarding Dogs (LGDs) in the context of historically human-dominated landscapes and reintroduction of grey wolf (Canis lupus) in Northern Europe (c.f. Boitani & Sutherland, 2015). The aim was to study local conditions on Estonian and Finnish Baltic islands and coastal areas, which are scattered habitats for wolves both concerning landscapes and human settlements - how different kind of LGDs, breeds, raising methods; generally the composition of the use of LGDs as working dogs with different kind of farm surroundings and farmers relate to the co-existence with wolves (Canis lupus).
Data collection conducted through visits to rural enterprises, mainly farms, semistructured interviews and interactive seminars including contacts and meetings with stakeholders during first phase 2007-2013 and second phase starting 2015. The main findings were that damage prevention with LGDs as one solution for social conflicts and enhance animal welfare is successful. Efforts are still needed depending on the background variables of the guarded areas, individual traits of LGDs and dog keepers possibilities to invest time in training.
In Estonia the use of LGDs decreased damages and it was reported increased overall animal welfare observations. Benefits for agritourism were observed and discussed. In Finnish costal area LGDs referred merely as a measure towards the fear of damages, any intruders or transmission of animal diseases. In Finland seemed to be more dualistic separate system concerning reintroduction of wolves (Linnell et al., 2015; VerCauteren et al., 2012).

References

Boitani, L., Sutherland, W.J., 2015. Conservation in Europe as a model for emerging conservation issues globally. Conservation Biology 0, 1-3.

Linnell, J.D.C., Kaczensky, P., Wotschikowsky, U., Lescureux, N., Boitani, L., 2015. Framing the relationship between people and nature in the context of European conservation. Conservation Biology 1-8.

VerCauteren, K.C., Lavell,e M.J., Gehring, T.M., Landry, J.M., 2012. Cow dogs: Use of livestock protection dogs for reducing predation and transmission of pathogens from wildlife to cattle. Applied Animal Behaviour Science 140, 128-136.

- P06 - USING MEASURES OF PERSONALITY TO INFORM HEALTH ASSESSMENTS

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Highlights:

This study used personality and behaviour to differentiate between dogs with and without experience of a pain causing condition. Dogs with experience of a pain causing condition differed from those without experience in their personality, aggression score and age.

Keywords: *behaviour; health; pain; personality; temperament*

Painful health conditions affect a high proportion of dogs worldwide posing a significant risk to their psychological and physical health. To date we don't have a clear understanding of how individual differences such as personality may impact pain behaviour in dogs. The aims of this research were (1) to determine whether dogs with and without experience of a pain causing condition could be differentiated by their personality and behaviour, (2) whether dogs with a current experience of a pain causing condition differed in their personality from those with historic experience. A retrospective cohort study design was used. An online survey collected information from dog owners about their dogs'; age, sex, behaviour and personality using the Positive and Negative Activation Scale (PANAS) for dogs. 867 complete surveys were used in the analysis. The personality components 'Energy & Excitement' (OR=0.25, p=0.03) and 'Adaptability' (OR=0.31, p=0.06) were negative predictors of pain experience. Total aggression (OR=2.01, p=0.02) and age (OR=1.07, p=<0.001) were both positive predictors of pain experience (Binomial logistic regression). Dogs with 'current' experience of a pain causing condition had lower Energy/Excitement scores compared with those with an 'historic' experience of a pain causing condition *W(199)=4,022, P=0.02* (Wilcoxon sum ranks test). These results provide insight into the association between pain and personality in dogs which may be potentially useful in veterinary assessments.

- P07 - DOGS' RESPONSES TO VISUAL AND AUDITORY CAT-RELATED STIMULI

C.L. Hoffman* (presenting), N. Roberts, S. Handley, M.K. Workman

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Highlights:

We tested dogs' responses to visual and auditory cat-related and control stimuli. Dogs oriented more to the auditory cat stimulus than to the visual cat stimulus. Dogs that had harmed small animals were more attentive to the cat sound than those that had not. It may be possible to use cat sounds to predict which shelter dogs will get along with cats.

Keywords: *behavioral assessment; cat; dog; perception*

Standardized assessments have been developed to assess dogs' behaviors around other dogs, but there currently is no way to predict how a dog in a rehoming shelter will behave around cats, unless the dog's previous history is known. This study explored dogs' responses to visual and auditory cat-related and control stimuli, and tested whether dogs known to interact safely with cats responded differently to the stimuli than dogs known to have injured or killed cats or other small animals. We video recorded 69 dogs' responses to the stimuli, and raters who were blind to the dogs' behavioral histories coded the dogs' reactions. Dogs differed in the amount of time they spent orienting to the cat and control visual stimuli and cat and control sounds, $\chi^2(3) = 108.58$, $p < 0.001$. Pair-wise comparisons indicated that the dogs spent significantly more time orienting to the cat sound than to the visual cat stimulus, to the visual cat stimulus than to the visual control stimulus, and to the control sound than to the visual control stimulus (for all, $p < 0.05$). Dogs that had killed or injured a cat or other small animal spent more time orienting to the cat sound than dogs that did not have this history ($Z = 2.52$, $p = 0.01$). The results indicate that dogs are more responsive to auditory than visual cat-related stimuli, and that it may be possible to use cat sounds to predict which shelter dogs are likely to fare well in homes with cats.

- P08 - BIOPSYCHOSOCIAL CHARACTERISTICS WHICH MAY PREDICT CONSERVATION SCENT DETECTION DOG SUCCESS

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Highlights:

We assessed features perceived to influence conservation scent detection dog success. A biopsychosocial framework was used to assess interview data and a review of literature. Certain psychological traits were perceived as important to all fields of scent detection. However, many biopsychosocial traits varied in importance depending on the field of scent detection.

Keywords: *behaviour; conservation; dog; scent-detection*

Scent detection dogs have been used in conservation for over 100 years. However, only recently have scientists begun to document how these dogs are used, and to evaluate their effectiveness. We undertook a literature review of conservation scent detection dogs, focusing on their capabilities, limitations, and applications, and investigating how they have been used and why they are so successful in some situations, yet fail in others. We applied a biopsychosocial framework to determine which characteristics were considered to be most predictive of success. While there is extensive literature on which traits are most commonly selected for, such as boldness, play/ food drive, persistence, and dominance, there is very little information on why these traits are important, or how they vary between different fields of scent detection. We then analysed interview data collected from 40 professional scent detection dog handlers and trainers, a subset of whom worked in conservation. We used the same biopsychosocial model to investigate which dog characteristics were thought to be associated with success in scent detection work. We found a great deal of variability in the perceived importance of different traits, such as environmental stability, independence, and certain physical features such as size and activity level, between different fields of scent detection work. Understanding which traits are most predictive of success in various fields of scent detection is necessary to improve selection, training, and deployment methods.

- P09 - DOGS KNOW SKILL LEVELS OF HUMANS

H. Chijiiwa[1],[2]* (presenting), E. Horisaki[3], H. Kuroshima[1], Y. Hori[1], K. Fujita[1]

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Highlights:

Dogs observed a person good at opening a container and another poor at it. They looked at and stayed near the former longer than the latter if the container had food. Dogs showed a reversed tendency if the container was empty. Dogs know skill levels of humans to maximize the chance to get food in the container.

Keywords: *affective evaluation; skill level; social evaluation; sympathy*

Dogs are sensitive to human behavior and they evaluate humans even from a third-party viewpoint (Chijiiwa et al., 2015). Here we tested whether dogs recognize how skilled a person is at a manual task. We showed dogs restrained lightly by their owner an action of two people; one was good at opening a lid to take an object out from a transparent container (skilled person) and the other poor at it (unskilled person). After showing this action twice with different containers, both actors tried to open another container which had food inside (Food condition; n=12), or nothing (Empty condition; n=12). During observation for 10 seconds, dogs looked at the skilled person significantly longer than the unskilled in the Food condition (p=0.04, U-test), whereas they tended to look at the unskilled in the Empty condition (p=0.05, ibid.). Furthermore, after being released, they first approached the skilled person in the Food condition (p=0.04, binomial test), whereas they approached randomly in the Empty condition (p=0.39, ibid.). The difference between the two conditions was statistically significant (p=0.04, Fisher). The result suggests that dogs can recognize skill levels of humans, and they behave differently according to the situation. When the action was linked to dogs' immediate benefit, they preferred the skilled person who was more likely to provide them with food. Instead they might have shown interest in the unskilled person from affective reasons such as encouragement or comfort when the action was irrelevant to their own benefit.

References

Chijiiwa, H., Kuroshima, H., Yusuke. H., Anderson, J. R., Fujita, K., 2015. Dogs avoid people who behave negatively to their owner: third-party affective evaluation. Anim Behav 106, 123-127.

- P10 - A COMPARISON OF TWO PARADIGMS FOR ASSESSING PROSOCIAL TENDENCIES IN PET DOGS

R. Dale[1],[2]* (presenting), M. Quervel-Chaumette[1], S. Marshall-Pescini[1],[2], F. Range[1],[2]

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Highlights:

Two tests investigating if dogs show prosociality towards conspecifics were directly compared. Dogs were prosocial to familiar, but not stranger, partners. Dogs were not affected by social facilitation in one study but were in the other. Overall dogs are prosocial to 'friends' but certain behaviors are not stable across methodologies.

Keywords: *cooperation; dog; methodology; prosociality*

Other-regarding preferences are considered to be the foundation of human cooperation. However, the evolutionary origin of this behavior in humans remains poorly understood. So far, comparative studies in primates have led to mixed conclusions probably due to methodological differences relating to both task complexity and the control conditions used. Here, we used two tasks; the bar pulling paradigm and a token choice task. Both required minimal cognitive demands, which ensured task understanding, and employed as similar as possible methods but differed in terms of reward visibility and the action employed by the subjects. In the bar pulling task dogs behaved prosocially by donating food to a conspecific, but only if the partner was familiar (familiar vs stranger; glmm: $z = -4.26$; $p < 0.001$). Moreover, by including a social control condition, we showed that in the bar-pulling task, the dogs' prosocial response was not due to a simple social facilitation effect (familiar-test vs familiar-control; glmm: $z = -2.39$, $p < 0.05$) but may have had an effect in the token test. Preliminary comparisons between the tasks show that in general dogs gave more food in the bar pulling than the token choice task, suggesting that food visibility may affect performance. Indeed, the social facilitation control with a stranger partner had a different influence in the two tasks (means; bar-pull: 13.1, token-choice: 8.3. Wilcoxon: $W=154$, $p<0.05$). These studies show the propensity for prosociality in dogs but also stress the necessity for caution when drawing conclusions from only one paradigm.

- P11 - EMOTIONAL CONTAGION IN DOGS (Canis familiaris) TO SOUNDS OF HUMANS AND CONSPECIFICS

A. Huber[1]* (presenting), C.A. Müller[1], A.L.A. Barber[1], T. Faragó[2], L. Huber[1]

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Highlights:

We conducted a playback study to investigate emotional contagion in dogs to emotional sounds. Emotional sounds originated from humans and dogs and included a negative and a positive valence. The valence of the stimuli had an intriguing effect on the behavioral response of the dogs. The responses to negatively valenced sounds seem to be most consistent with emotional contagion.

Keywords: *domestic dogs; emotional contagion; empathy; playback study*

Dogs are of exceptional significance for investigating empathy as they are so far the only non-primate species indicating cross-species empathy with humans. This study applied a playback experiment to investigate emotional contagion, a basic component of empathy, in dogs. We contrasted non-emotional sounds from the dogs' environment with emotional sounds of humans and conspecifics that comprised stimuli with negative and positive valence. For a response interpreted as emotional contagion, the emotional tone of the dogs' behavior has to correspond to the valence of the emotional sound. Consequently, in response to emotionally negative sounds, dogs should increasingly express behaviors indicating negative emotions; this should not be the case for positive sounds. Behavioral indicators for negative emotional states were freezing and a Relative Reactivity Score (RRS) comprising of several negative arousal behaviors. The subjects showed increased attention to emotional compared to non-emotional sounds. Although the response towards emotional sounds of both species was similar, dog sounds, independent of their valence, generally induced more freezing behavior. Independent of species, both behavioral indicators for negative emotional states were significantly increased after negatively valenced sounds compared to positively ones. The findings indicate emotional state-matching in dogs for negative sounds of both species, which suggests emotional contagion. Besides, the study provides a first approach for investigating empathy for positive affective states in dogs.

- P12 - THE INFLUENCE OF AGE, BREED, SEX AND PREVIOUS EXPERIENCE ON DISCRIMINATION LEARNING & INFERENCE BY EXCLUSION IN PET DOGS

C. Schwarzl[1]*(presenting), M. O´Hara[1,2], L. Huber[1], L. Wallis[1,2]

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Highlights:

Older dogs took longer to learn the discrimination and older females showed reduced inference ability. Dogs with previous experience were faster to learn the discrimination and no breed difference was found. 50% of younger dogs showed inference by exclusion above chance in comparison to 22% of older dogs. Learning ability predicted inference by exclusion performance.

Keywords: *age; dogs; exclusion; inference; touchscreen*

The ability to infer by exclusion, defined as selection of the correct alternative by logically excluding other potential alternatives (Call, 2006) has been found in many non-human animals. Wallis et al., (2016) reported a decrease in discrimination learning with age and an increase in inference by exclusion ability in Border Collies utilising a touchscreen. A learning effect during non-rewarded test trials could explain why younger dogs performed poorly, therefore we aimed to test a novel approach (O'Hara et al., 2015), which permitted rewarded test trials. Two breed groups; Border collies (N=18) and other breeds (N=25) were tested on a touchscreen for discrimination learning and inference by exclusion ability. Two age groups were examined <6 years (M=11, F=11) and > 6 years (M=10, F=11), and dogs were additionally divided into touchscreen experienced (N=18) and unexperienced (N=25). Each dog was trained on a novel stimulus pair (S+ and S-) to a two stage criterion, when testing for inference by exclusion commenced. Results showed that older dogs took longer to learn the discrimination ($p=0.004$), and dogs with previous experience learnt faster ($p=0.010$). Female dogs displayed a reduced ability to infer by exclusion with age in comparison to males, and younger dogs were twice as likely to use inference by exclusion as older dogs. Dogs that required fewer sessions to reach criteria were more likely to infer by exclusion. Our results support previous studies on age effects on discrimination, however, when using this novel approach, inference by exclusion declined with age in female dogs.

References

Call, J., 2006. Inferences by exclusion in the great apes: the effect of age and species. Anim Cogn 9(4), 393–403.

O'Hara, M., Auersperg, A.M.I., Bugnyar, T., Huber, L., 2015. Inference by Exclusion in Goffin Cockatoos (Cacatua goffini). PLOS One 10(8), e0134894.

Wallis, L. J., Virányi, Z., Müller, C. A., Serisier, S., Huber, L., Range, F., 2016. Aging effects on discrimination learning, logical reasoning and memory in pet dogs. Age 38(1), 6.

- P13 - THE FUNCTION OF HUMAN BODY LANGUAGE DURING DOG TRAINING

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Highlights:

Factors that may facilitate dogs' learning despite delayed positive reinforcement were investigated. Owner-dog dyads were filmed during training and the timing of people's actions were measured. Following dogs' responses, people usually made a body movement prior to intentional reinforcement. Such movements likely become conditioned reinforcers, with implications for research and practice.

Keywords: *communication; conditioned reinforcement; reinforcement; training*

Delayed positive reinforcement is detrimental to learning but common in dog training (Browne et al., 2013). Despite this, training is often successful. This study investigated factors that could aid learning despite the delays. Videos of 21 people training their dogs (287 trials) were examined for the timing of the dogs' responses and the people's actions. In 75% of trials the person made a body movement, and in 21% of trials they gave verbal praise or a click, immediately following a dog's response, confirming the findings from subset of these data (Browne et al., 2014). Hand movements or a change in body position, both related to food delivery, were the most frequent (82% and 9% respectively) initial body movements and could have served as signals. In the most common sequence of events the average delay between a dog's response and the person's first body movement was 0.32 s, followed by 0.24 s to verbal praise, and then 0.83 s to food delivery. Because the initial body movements were delivered consistently and rapidly (before the intended reinforcers), they likely functioned as signals. Such signals may facilitate learning in situations with poor temporal contiguity and become conditioned reinforcers. This may also account for the findings from studies showing no learning advantage when comparing clicker training to food delivery alone (e.g., Smith & Davis, 2008), as body moments related to food delivery may become conditioned reinforcers. It is important to take account of all body movements during training in such research and in practice.

References

Browne, C.M., Starkey, N.J., Foster, T.M., McEwan, J.S., 2013. Delayed reinforcement – Does it affect learning? J Vet Behav 8, e37-e38.

Browne, C.M., Starkey, N.J., Foster, T.M., McEwan, J.S., 2014. Dog training: Reinforcement timing and owner body language. J Vet Behav 9, e17.

Smith, S.M., Davis, E.S., 2008. Clicker increases resistance to extinction but does not decrease training time of a simple operant task in domestic dogs (*Canis familiaris*). Appl Anim Behav Sci 110, 318-329.

- P14 - IDENTIFYING AND INTERPRETING SCATS OF SYMPATRIC CANIDS IN AUSTRALIA

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Highlights:

We tested major assumptions involved in scat identification and analysis in Australia. Scats from domestic dogs with controlled diets were analysed. We suggest that current methods for scat identification are unreliable. This may be leading to inaccurate reports of feeding behavior and intraspecific predation.

Keywords: *diet; dingo; predation; scat*

Dingoes/wild dogs (*Canis dingo/familiaris*) and red foxes (*Vulpes vulpes*) are common carnivores across most of Australia. The feeding behaviour of these canids are difficult to observe in the wild, therefore scientists rely on scat analysis. Effective scat analysis necessitates accurate identification of both the species responsible for depositing the scat, and of the items found in the scat. In an Australia wide review of 41 papers that collectively identified and analysed 29842 dingo scats, we found that authors customarily relied on size, shape and smell for scat identification. To confirm the species-level identification, the presence of grooming hairs is often used. Grooming hairs are loosely defined as presence of <10 hairs, indicative of ingestion while grooming, compared to 10 or more hairs, indicative of predation. To test this assumption we are analysing the scats of domestic dogs on a controlled diet to record the presence and numbers of grooming hairs. Currently, we have analysed 90 scats from 19 domestic dogs. Our preliminary results show that 89% of scats contained >50 grooming hairs. Despite the prevalence of grooming hairs in domestic dog scats, grooming hairs were only reported in 0.7% scats reviewed. These results suggest the presence of ≥ 10 hairs does not necessarily indicate predation. Therefore, reports of intraspecific predation may be over-estimated in the literature. We recommend that the identification of scats and presence of grooming hairs be accurately recorded in the literature and caution taken when interpreting data from analysed scats.

- P15 - GENETIC DIFFERENTIATION BETWEEN DOG BREEDS AND BREED VARIETIES

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Highlights:

The population structure of related breeds and breed varieties was analyzed using microsatellites. They failed to show clear differentiation between the different groups. Results indicate that separation into breed varieties is artificial. Matings across varieties can be beneficial to maintain genetic diversity within these breeds.

Keywords: *breed varieties; discriminant analysis of principal components; dog; population structure*

Breeding practices and registration restrictions influence the population genetic structure of modern dog populations by creating the so-called breed barrier rule. Currently, the Fédération Canine Internationale (FCI) recognizes 343 different breeds and 122 breed varieties. The strict breed standards have established closed genetic pools within each breed promoting the reduction of the genetic diversity. Phenotypic selection based on morphological appearance can create within-breed subgroups or breed varieties. In Belgium, some breeds may present separate subgroups or are closely related to other breeds, such as the Belgian Griffon dogs (Griffon Bruxellois, Griffon Belge and Petit Brabançon), or the different coat varieties in the Cavalier King Charles spaniel among others. Using 19 microsatellite markers we evaluated the population structure and determined similarities between 23 closely related breeds and breed varieties using discriminant analysis of principal components, implemented in the DAPC package in R.
The results showed no genetic differentiation between the three Griffon breeds. In the Cavalier King Charles Spaniel, the practice of avoiding matings between animals of different colors (parti-color and whole-color) did not lead to differentiation into subpopulations. These results indicate that separation into breed varieties is artificial at the neutral molecular marker level. The effect of combining varieties within a breed is strongly breed-dependent. Matings across varieties can be beneficial to maintain genetic diversity in breeds where this is problematic.

- P16 - RECOGNIZING EMOTIONS IN VOCAL COMMUNICATION, BETWEEN DOGS AND HUMANS

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Highlights:

We studied, which variables are involved in recognizing emotions in vocalizations of dogs and humans. We confirmed our earlier results on a wider international sample. We found that intensity of the vocalizations is affected by pitch related parameters, positively. Valance is influenced by time related parameters, negatively.

Keywords: *dog; emotion; human; vocal communication*

A growing body of evidence suggests that the mechanisms of emotion expression and recognition are shared across mammals (Andics et al., 2014). In a recent study we found that fundamental frequency and call length of human and dog vocalizations affect how 36 Hungarian participants perceived their emotional load (Faragó et al., 2014). To further study the generalizability of these results, in this study 973 participants from 68 countries (mainly Hungarians and Americans) listened 100-100, 2s dog and human vocalizations, and rated them on valence and intensity scales. We measured 50 acoustical parameters in the vocalizations, formed factors with PCA, and applied linear regressions to test their effect on the ratings. In both dog and human vocalizations valence was affected negatively by the Time domain factor, containing call length and other time related parameters (dog: $B=-0.458$; $p<0.001$; human: $B=-0.286$; $p=0.003$), while Pitch factor containing fundamental frequency related ones affected intensity positively, (dog: $B=0.264$; $p=0.002$; human: $B=0.486$; $p<0.001$). Comparing USA with Hungarian subjects, we found that Americans tended to rate vocalizations to be more positive in all contexts (country*context: $F(2,56789)=4.783$; $p=0.008$) and this was the case within species too (country*spec: $F(2,56789)=14.496$; $p<0.001$). Americans rated all contexts to be more intense in case of human sounds (spec*context*country: $F(2,56793)=5.802$; $p=0.003$). Hungarian subjects rated all dog vocalizations to be more intense, Americans rated positive human sounds higher on intensity scales than dog vocalizations. Summing up, we confirmed our earlier results on an international sample, and found some new factors and background variables behind this phenomena.

References

Andics, A., Gácsi, M., Faragó, T., Kis, A., Miklósi, Á., 2014. Voce-Sensitive Regions in the Dog and Human Brain Are Revealed by Comparative fMRI. Curr Biol 24, 574-578.

Faragó, T., Andics, A., Devecseri, V., Kis, A., Gácsi, M., Miklósi, Á., 2014. Humans rely on the same rules to assess emotional valence and intensity in conspecific dog vocalizations. Bio Lett 10, 20130926.

- P17 - DANGEROUS DOGS? IMPULSIVITY IN THE BRAZILIAN MASTIFF (FILA BRASILEIRO)

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Highlights:

Impulsivity is subject to artificial selection in working dogs and includes element of aggressivity. We compared impulsivity levels between dog breeds with different work selection purposes. We focused on the Brazilian Mastiff, which is banned in the UK as a "dangerous dog" breed. Brazilian Mastiff scored significantly higher than Labrador Retrievers for overall impulsivity.

Keywords: *Brazilian Mastiff; Fila Brasileiro; dog behaviour; impulsivity*

Level of impulsivity may reflect historic and recent artificial selection in dogs for different work purposes. There is large differentiation of this trait between dog breeds consistent with their working lines, but also large behavioural variation within each breed (Fadel et al., 2016). In this study we compared impulsivity levels in dogs as measured by the Dog Impulsivity Assessment Scale (DIAS), a thoroughly validated psychometric scale (Wright et al., 2011). Between and within breed comparisons were done among common pet breeds in the UK (e.g. Labrador Retrievers, Border Collies, Arctic breeds) and the Brazilian breed Fila Brasileiro (FB). The FB has been specifically selected for its aggressive and guarding behaviour and is banned in the UK under the Dangerous Dog Act. We collected over 2000 DIAS questionnaires from British dog owners covering several breeds and 70 from FB breeders in Brazil. FB scored higher than Labrador Retrievers on average for overall impulsivity (Tukey post-hoc tests $p=0.008$), but were not significantly different to Border Collies or Arctic breeds (Tukey post-hoc tests $p>0.05$). Analysis of the DIAS factors (1. behavioural regulation, 2. aggression threshold and response to novelty, and 3. responsiveness) yielded some significant results in pairwise breed comparisons which can be related to the working selection of each breed. Given the high variation within breeds and few significant results of between breed comparisons, these results emphasise the risks of making behavioural generalisations about an individual dog based only on its breed.

References

Fadel, F.R., Driscoll, P., Pilot, M., Wright, H., Zulch, H., Mills D.S., 2016. Differences in trait impulsivity indicate diversification of dog breeds into working and show lines. Sci Rep 6, 22162.

Wright, H.F., Mills, D.S., Pollux, P.M.J., 2011. Development and validation of a psychometric tool for testing impulsivity in the domestic dog (*Canis familiaris*). Int J Comp Psychol 24, 210–225.

- P18 - SHAPING DOG BEHAVIOR WITH PRIMARY AND SECONDARY REINFORCERS

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Highlights:

We compared immediate food reward to clicks and saying "chee" in training dogs to sit and stay. Dogs trained with immediate food learned to sit faster than those trained with secondary methods. These results are in line with laboratory studies on many species. The best form of reinforcement to use in training dogs likely depends on many factors.

Keywords: *behavior; clicker; dog; reinforcement; shaping*

In recent years many dog trainers have replaced aversive methods with those based on positive reinforcement. Surprisingly few experiments have been carried out systematically comparing the efficacy of different forms of positive reinforcement in shaping commonly-desired behaviors in dogs. In this study, we compared immediate tangible positive reinforcement (a small piece of commercial dog treat), with two forms of secondary reinforcement: a vocal sound ("chee"), and the click of a device commonly used for this purpose. Each of the secondary reinforcers had previously been established by Pavlovian pairing with a primary reinforcer (dog treat), and was always followed promptly by a dog treat during the shaping exercise. The subjects were 100 young adult dogs available for adoption at a local animal shelter. To our knowledge, these dogs had no previous experience with any form of behavioral training. Each was trained to sit and stay, and the maximum duration of stay achievable in a set training period was compared across groups. The group receiving only primary reinforcer reached a higher criterion of training than the group trained to a verbal secondary reinforcer ($p < 0.05$). Performance of the group experiencing a clicker secondary reinforcer was intermediate between the other two groups, and not significantly different from either. These results are in line with what would be predicted from laboratory studies on conditioning and raise important questions about the best conditions in which to use different forms of reinforcement.

- P19 - WHAT "COUNTS" FOR DOGS IN A FOOD CHOICE TASK?

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Highlights:

Dogs were presented with a spontaneous choice between two quantities of food items. Dogs chose the larger amount of food irrespective of the number of items. Individual item size did not affect dogs' choices. These results suggest that amount, rather than numerosity, plays a primary role in food choices.

Keywords: *dog; numerical competence; quantity judgement; spontaneous discrimination*

Numerous studies have shown that animals can discriminate quantities of more or less food. However, little attention has been given to the relative salience of numerosity compared to the total amount when animals are making their choices. Individual item size may also influence animals' preference, as reported in chimpanzees. Here we used one of the most widely adopted paradigms to investigate quantitative abilities in vertebrates, the food choice task, to assess which information is spontaneously used by dogs to discriminate between two quantities of treats. Nine domestic dogs were given choices between two sets of food items in three conditions differing in the correlation between numerosity and the total amount (i.e., volume). In the Congruent condition, the more numerous set had the largest amount of food; in the Incongruent condition the more numerous set had the smallest amount of food; in the Controlled condition the amount of food between the two sets was equalized. Dogs significantly selected the set containing the larger amount of food both in the Congruent ($t(8) = 5.69$, $p < 0.001$) and in the Incongruent condition ($t(8) = 7.86$ $p < 0.001$) whereas no preference was observed in the Controlled condition ($t(8) = 0.46$ $p = 0.661$). The presence of the largest individual item in a set did not bias dogs' choices.
Results show that dogs based their choices on the total amount of edible food rather than on the number of food items, suggesting that, in food choice tasks, amount counts more than number.

- P20 - COMPARISON OF SOCIO-COGNITIVE SKILLS AMONG ASSISTED THERAPY DOGS AND PET DOGS

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Highlights:

Compared with pets dogs, assisted therapy dogs have a longer duration of gazing at the face of a person as a communicative response when reinforcement is inaccessible to them, and also have a greater persistence of this response when it no longer leads to reinforcement. This highlights the importance of training communicative behaviors, like gazing, in dogs that perform this type of work.

Keywords: *animal assisted therapy; communication; dogs; gaze; inhibitory control*

Animal Assisted Therapies involve spontaneous and unregulated visits, where the dog interacts with the patient. The goal is that the patient benefits from this positive interaction. Despite how promising these interventions may seem, there are few studies of effectiveness and socio-cognitive profiles of these dogs. We aimed to compare the performance of pet dogs and assisted therapy dogs in several socio-cognitive tasks, so as to detect the most relevant areas for the achievement of this work. For that purpose, we evaluated eight dogs participating in assisted activities in a palliative care service and an acute psychotic patients service, and a control group of seven pet dogs which lived in the same family houses of the aforementioned group, but do not participate in the assisted activities. We administered a test battery in a counterbalanced order across dogs: sociability to a stranger, learning to gaze at the human face when reinforcement is inaccessible, A-not-B task and DIAS questionnaire. The results showed that, compared to pet dogs, assisted therapy dogs gaze more at people faces, both in the baseline and in the extinction phase when they do not longer receive reinforcement. No differences were observed in the other tests. These results suggest that persistence of communicative responses is essential for dogs to perform assistance activities, so it should be stimulated through specific training.

- P21 - CHILD-FAMILY DOG INTERACTIONS IN CHILDREN UP TO SIX YEARS AND CAREGIVERS' ATTITUDES TO SUPERVISION

C. Arhant[1]*(presenting), R. Landenberger[1], A. Beetz[2],[3], J. Troxler[1]

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Highlights:

402 dog owners with children up to six years participated in an online-survey. Dog owners often do not comply with common recommendations on supervision of child-dog interactions. Often they see a low need to prevent risky interactions with their family dog. Regarding intervention in interactions low agreement with experts in dog bite prevention is reached.

Keywords: *child-dog interactions; dog bite prevention; parent supervision*

Dog bites suffered by young children are often inflicted by the family dog and preceded by an interaction. As poor supervision of child-dog interactions may be a key cause of these incidents, we set out to investigate everyday child-dog interactions observed by parents and their attitudes to supervision.
An online survey was conducted over a four-month period. To take part, respondents (N=402) had to live with a child (≤6 years) and to own a dog. The questionnaire contained sections about demographics, child-dog interactions, supervision/daily management and intervention in interactions (scale: 1-6). Questions about intervention included five pictures which were chosen based on concordant expert ratings.
Frequently observed interactions were interactions that are commonly seen as positive such as "child pets the dog" but might also be perceived as a threat by the dog (Mean: 5.05, S.D.: 1.27). Respondents' average level of toleration of unsafe behaviours was in the middle of a scale from one to six, (3.05, S.D.: 1.29), and their level of attentiveness was similar (Mean: 3.12, S.D.: 1.47). Respondents rated the need for an intervention in child-dog interactions very differently than experts ($U=-13.52$, $p<0.001$): on average, participants agreed with experts on only two depicted situations involving the family dog and on four encounters with an unfamiliar dog.
Overall, dog owners need to improve their supervision of child-dog interactions. It is vital to educate caregivers about potentially unsafe behaviours and safety measures to use with the family dog.

- P22 - DO DOGS RECOGNIZE INTENTION AND GOAL OF HUMANS?

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Highlights:

Dogs' recognition of human intention and goal was tested with an expectancy violation method. A responder brought to the requester either the item claimed or the one not claimed (violation). The requester either thanked or blamed the responder, either congruently or not with his claim. Dogs watched the violator longer but were insensitive to congruency of the outcome.

Keywords: *expectancy violation procedure; intentionality; mind reading; social intelligence*

We tested whether dogs recognize intention and goal of humans using an expectancy violation procedure involving no food reward. The owner lightly restrained the dog. In the first phase, a human requester asked a responder to bring one of the two objects by three repeated pointing. The responder either brought to the requester the object claimed (follower) or the one not claimed (violator). Then in the second phase that followed, the requester either thanked or blamed the responder with words accompanied by corresponding facial expression, either congruently with the claim or not. Thus there were four different sequences of acts: 1) the follower of the claim was thanked (congruent outcome); 2) the follower was blamed (incongruent outcome); 3) the violator of the claim was thanked (incongruent); 4) the violator was blamed (congruent). All 24 dogs experienced the four actions once in a counterbalanced order. We analyzed the duration of dogs' gaze toward the responder during the first phase and that toward the requester during the second phase. Results showed that dogs watched the responder reliably longer in the first phase but there was no differential effect of the outcome shown by the requester's reactions. These results suggest that dogs recognize the responder should follow the requests but may not know the requested item is the one that the requester wants.

- P23 - SIZE DISCRIMINATION IN DOMESTIC DOGS

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Highlights:

Dogs were tested on ability to perform a simultaneous size discrimination task. All eight dogs could discriminate circles 20% (12.6mm) different in diameter. Four of eight dogs could discriminate circles 10% (6.3mm) different in diameter but not 5% (3mm). Factors affecting individual variability in dog discrimination performance should be investigated.

Keywords: *discrimination threshold; dog; size; visual perception*

A number of recent studies have required dogs to perform visual discrimination tasks presented on a computer monitor; however, surprisingly little is known about the limits of their visual discrimination capabilities. We trained dogs (n=8) on a simultaneous size discrimination task using black circles presented on an LCD screen. Circle pairs presented in this study were equidistant in diameter from a reference circle (207 pixel diameter, approximately 62.1 mm). All eight dogs were able to successfully discriminate between circles that differed in diameter by 20% (42 pixels, approximately 12.6 mm) (accuracy range: 72% - 88%; individual binomial tests all $p < 0.001$). Four of the eight dogs were able to discriminate between circles 10% different in diameter (21 pixels, approximately 6.3 mm) (accuracy range: 63% - 72%; individual binomial tests $p \leq 0.026$), but none were able to discriminate circles 5% different in diameter (10 pixels, approximately 3 mm) (accuracy range: 52% - 58%; individual binomial tests $p \geq 0.123$). These results suggest that dogs can be reliably trained to discriminate between circles based on size; however, individual differences are present in discrimination performance. Further research into factors that contribute these differences could enhance our understanding of dog performance in more applied discrimination tasks.

- P24 - PSICHIATRIC PATIENTS AS RANDAGIAMOTM VOLUNTEERS IMPROVE THE QUALITY OF LIFE OF SHELTER'S DOGS

B. Boccini[1], D. Catillo[2], L. Menchetti[1], C. Amato[2], S. Diverio[1]* (presenting)

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Highlights:

RandAgiamo™ program provides training and socialization of shelter dogs. Psychiatric patients acting as volunteers become themselves providers of care for shelter dogs. Walking together promoted social relationships among humans and dogs. Psychiatric patients contributed to improve the quality of life of shelter dogs.

Keywords: *psychiatric patient; shelter dog; walking dogs*

Scientific literature showed dogs could play a role of co-therapist reducing depression, stress disorder symptoms, and anxiety in human patients. In the shelter context, these roles can be reversed since the dogs themselves need of social enrichments and inter-specific contacts. RandAgiamo™ is a project aimed to increase dogs' adoption rate and welfare by implementing a standardized training and socialization protocol (Menchetti et al., 2015). Volunteers walk dogs that successfully complete this program. Conversely to usual life, where they were always the object of health care or treatments, RandAgiamo™ provided to some psychiatric patients the opportunity to become themselves the providers of care for someone else. Since 2012, the patients, together with their health operators, were assigned to the role of volunteers. They regularly visit the shelter for walking RandAgiamo™ dogs to help them maintaining skills acquired with training. Walking together promoted social relationships among humans and dogs, but also provided an opportunity to be in contact with nature. The project brought overall tangible benefits. Walking dogs contributed to increase relational and technical competencies, social integration and self-esteem in psychiatric patients. On the other hand, their volunteering to the shelter provided a social, recreational and experiential enrichment to the dogs. Patients refereed to be highly satisfied of their experience as volunteers. This is proven by their assiduous participation and from their feeling of proud to be part of RandAgiamo™. Their collaboration brought a consistent improvement of the quality of life of the shelter dogs of which they took care.

References

Menchetti, L., Mancini, S., Catalani, M.C., Boccini, B., Diverio, S., 2015. RandAgiamo™, a Pilot Project Increasing Adoptability of Shelter Dogs in the Umbria Region (Italy). Animals 5(3), 774-792.

- P25 - DOG-HANDLER DYNAMICS INFLUENCE AVALANCHE SEARCH TEAM'S PERFORMANCE

G. Riggio[1] (presenting), C. Azzari[1], M. Iaboni[2], L. Menchetti[2], R. Zasso[3], A. Cagnati[3], F. Dallo[4], W. Di Mari[5], M.M. Santoro[5], S. Diverio[2]*

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Highlights:

Dynamics between dog and handler during a simulated avalanche search trial were evaluated. Three principal components described dog's orientation, spatial position and handler-directed behaviors. Visual and physical contacts between dog and handler were associated to low performance.

Keywords: *avalanche dog; dog-handler relationship; search performance*

Avalanche search dogs represent an irreplaceable resource in case of environmental disasters. The "Alpine Rescue of Guardia di Finanza Project" is a broad research project aimed to identify limiting factors affecting teams' performance. This work focused on behavioral dynamics between dog and handler during a simulated avalanche search trial. A warmed up scent article was randomly buried under the snow (-20cm), avoiding olfactory pollution, in fields prepared to resemble an avalanche fall environment (10mt x 15mt; 2170masl). Twelve dog-handler Units were individually video recorded and videos were analyzed through focal animal sampling of behavioral categories related to the dog-handler relationship (dog-handler tactile and visual communication, reciprocal position and distance). Nine of the 20 trials analyzed (45%) were successful with a mean latency of 148s. Principal component analysis included 15 behavioral traits and extracted three principal components (PCs) explaining 71% of the variation. PC1 mainly included items describing orientation of the dog compared with the handler and vice versa. PC2 included items related to dog's spatial position within the field in relation to its handler. PC3 included handler-directed behaviors of the dog. High score of PC3, indicating frequent visual and physical contacts, reduced the likelihood of success (odd ratio= 0.144; 95% CI= 0.034–0.612; p=0.009). These findings suggest the dog's behaviors directed to the handler may indicate insecurity during an avalanche search and negatively affect team's performance. Dogs less dependent on their handlers spent more time interacting with the environment and performed better during the avalanche search trial.

- P26 - INTRASPECIFIC ATTACHMENT IN DOGS: IS THE MOTHER ALWAYS THE MOTHER?

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Highlights:

Scientific literature on intraspecific attachment in dogs is scarce. Thirty-nine adult dogs were tested in a modified version of the Ainsworth's strange situation test. Dogs were tested with their mother or an older cohabitant dog, both living in the same household. A slight preference for the mother was observed, but not a stronger bond.

Keywords: *attachment; bond; dog; intraspecific; mother*

Scientific literature on attachment in domestic dogs has mainly focused on dog bond toward humans. Despite the relevance of social relationships in the canine species, studies on intraspecific attachment are scarce. The aim of the current study was to assess whether in adult dogs the bond toward the mother is different from the bond toward another cohabitant dogs. Seventeen dogs (52.9% females, 38.9±13.3 months old, different breeds) were tested in a modified version of the Ainsworth's strange situation test where the stranger was played by a female stranger and the attachment figure was played by dogs' mother, living in the same household. A second sample of 22 dogs (45.5% females, 39.2±26.6 months old, different breeds) underwent the same test with an older cohabitant dog. The duration of dogs' social and non-social behaviors of the two samples in each episode was compared using the Mann-Whitney U test ($p < 0.05$). No difference was found between the two groups in the isolation episode; a few differences were observed for non-social behaviors throughout the test. A slight preference for the mother was observed in episodes after reunion (more approach and visual orientation). However, the findings do not fully support the hypothesis that the bond of adult dogs toward conspecifics sharing their daily life is stronger in case the conspecific is their own mother rather than another older dog. Future research should investigate more in depth this kind of bond, its features and its relationship with dog behavior and social life.

- P27 - SIX IN-DEPTH CASE STUDIES OF UNSUCCESSFUL GUIDE DOG PARTNERSHIPS

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Highlights:

Case studies of unsuccessful guide dog partnerships investigated the causes of premature retirement. Guide dog partnerships require compatibility between the dog and owner in various areas. In each case the pair were incompatible in one of these areas therefore the partnership broke down. The factors highlighted can be used for future matching of guide dogs and owners.

Keywords: *guide dogs; human-animal bond; human-dog relationships*

Guide Dogs is the largest guide dogs school in the world, qualifying over 800 guide dog partnerships per year. Up to 15% of partnerships may end prematurely due to behavioural problems in the dog, but there is a lack of research into the reasons for premature retirement. This study adds an important contribution to addressing this gap in knowledge. Six case studies were conducted on guide dog partnerships that worked together for less than three years. In each case the guide dog owner, puppy walker and re-homer were interviewed about the partnership and the dog. Thematic analysis of these accounts and content analysis of reports written by guide dog staff on the partnership was undertaken. The analysis of multiple sources of data helped to identify what may have led to the dog's retirement in each case and cross case analysis highlighted themes across cases. The findings highlighted the complex nature of the partnership and the need for compatibility between the pair in their work as well as their social and home environments. In each case, whilst most components of the relationship worked well, when one of these wasn't working it led to the breakdown of the partnership. These results illustrate the multitude of factors that need to be considered when matching a guide dog and owner. This could also be applied to other assistance dogs partnerships, as well as re-homing dogs from animal shelters. The study demonstrates the importance of acknowledging both the owner and dog in human-dog dyads.

- P28 - SIMILAR RECENT SELECTION CRITERIA CAUSED DIFFERENT BEHAVIORAL EFFECTS WITHIN GOLDEN AND LABRADOR RETRIEVER DOGS

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Highlights:

We studied the effects of recent selection on dog behavior using golden and Labrador retriever. Dog Mentality Assessment results for 2574 dogs classified as either common or field type were used. The selection lines showed different behavioral profiles despite similar selection criteria. Behavior components may thus be determined by different genetic architectures between the breeds.

Keywords: *behavioural genetics; behavioural test; dog behaviour; retrievers; selection*

Some dog breeds have been divided into divergent types due to different interests of breeders, and such types are interesting models for behavior genetics. The aim of this study was to determine the behavioral differences between the selection lines of golden and Labrador retriever. These breeds show a similar split where one type is bred for pet and conformation (common) and one for hunting (field). Our hypothesis was that the behavioral profiles of the types would be similar in the two breeds. Pedigree data and results from the Swedish Dog Mentality Assessment for 902 goldens (698 common and 204 field) and 1672 Labradors (1023 and 649) were used. Principal component analysis revealed six components: curiosity, play interest, chase proneness, social curiosity, social greeting and threat display. Breed and type affected all components, but interestingly, there was an interaction between breed and type for most of them. For example, in Labradors, the common type had higher curiosity than the field type ($F_{(1,1668)} = 18.359$; $P < 0.001$), while the opposite was found in goldens ($F_{(1,897)} = 65.201$; $P < 0.001$). Heritability estimates showed considerable genetic contributions to the behavioral variations, but also varied within breeds, suggesting different selection pressures. To exemplify, in Labradors, the heritability for curiosity was 0.18 in the common type and 0.54 in the field type. In conclusion, in spite of similar genetic origin and similar recent selection criteria, types behave differently. Traits not directly targeted by the selection criteria may thus be determined by different genetic architectures.

- P29 - A REVIEW OF ASSISTANCE DOG EFFECTIVENESS AND IMPLICATIONS FOR ANIMAL WELFARE

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Highlights:

Assistance dogs improve functioning for people living with disability. Existing scientific literature relies heavily on owner reports, which could reflect a placebo effect. Discussion of animal welfare concerns would be useful.

Keywords: *assistance dog efficacy; assistance dog welfare; disability support*

Assistance dogs (ADs) provide psychological and/or physical benefits to individuals with disability. In addition to guide dogs for the vision- or hearing-impaired, dogs assisting people with physical disabilities may retrieve objects for mobility-impaired owners, or notify their diabetic owner of potentially dangerous changes in blood sugar levels. They may also help people on the autism spectrum engage in social interactions, or give people with post-traumatic stress disorder confidence to go about daily activities without fear. However, available scientific literature on the effectiveness of ADs shows mixed results, and often relies on whether the owner perceives an improvement in functioning, which could be explained by a placebo effect. Some studies do not incorporate adequate controls, which could mean that a spurious variable is responsible for any observed improvement in functioning. Also, there is little examination about how this sort of work may impact the dog's welfare. The aim of this presentation is to provide an up-to-date review of existing scientific literature about AD effectiveness. Limitations of existing research will be examined, ways to improve controls in future studies suggested, and welfare issues for assistance dogs discussed. These suggestions will be useful to researchers seeking to design well-controlled studies with ADs, and to government agencies charged with funding disability supports.

- P30 - ODOR CATEGORIZATION IN DOGS

H.F. Wright[1], A. Wilkinson[1], D. Graham[1], R. Harding[1], H. Hodkinson[1], B. Keep[1], N.R. Cracknell[2], R.S. Croxton[3], H.E. Zulch[1]* (presenting)

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Highlights:

The ability of dogs to categorize odors was investigated. Experimental dogs succeeded in learning 40 odors (20 S+, 20 S-) divided into two categories. Dogs trained on the same odors without a categorical rule could not reach learning criterion. Experimental dogs could generalize the categorical rule to novel odors.

Keywords: *accelerant; categorization; dog; generalize; odor*

The ability to identify a novel stimulus as a member of a known category allows an organism to respond towards it in an appropriate way. Categorization can thus be considered a fundamental component of cognition and an essential tool for processing and responding to unknown stimuli. As this process is considered essential for interpreting and responding to stimuli in nature, it is likely to hold across species and sensory domains. The aim of this study was to examine whether dogs were able to categorize odors. Dogs were trained to discriminate 40 odors (20 S+ and 20 S-). The dogs in the experimental group (n=6) were rewarded for responding to substrate plus accelerant, burned and unburned and compared to the same substrates without accelerants (S+ counterbalanced). The control group (n=5) were trained on the same stimuli but without the categorical rule. Four experimental dogs reached learning criterion (average trials to criterion 538) whereas none of the control animals successfully learned the task in over 1000 trials. Further, the experimental group generalized their learning to untrained probe stimuli. These findings support the hypothesis that dogs are able to form an odor category and are able to use this information to generalize responses to novel odors of the same category. This suggests that investigating the principles of categorization in an applied setting may aid in the training and hence performance of working animals, such as explosive detection dogs.

- P31 - AGE, EXCITABILITY AND SPEED: AUTOMATED MEASUREMENTS OF BEHAVIOUR TRAITS IN AGEING RESEARCH

E. Kubinyi[1],[2]*(presenting), M. Nagy[3], J.J. Ablenado[1], R. von Hoof[1], T. Vicsek[4]

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Highlights:

Excitability can be measured by both a questionnaire scale and high frequency GPS loggers. This indicates that the excitability personality trait can be assessed automatically. Excitability and walking speed decreases with age.

Keywords: *ageing; excitability; GPS; leadership; personality*

Behavioural studies looking at the effect of age-related changes provided contradictory results in connection with activity. In the present study we collected trajectory data with high frequency GPS loggers about 50 dogs (25 pairs) and their owners during off-leashed walks and runs. Mean age of dogs was 4.4 (+/- 3.21) years, age varied between 0.6 and 13 years. Owners filled out a questionnaire about the personality of their dogs. The excitability trait was characterized by three items (dog is boisterous; seeks constant activity; not tends to be calm). With age both the speed of dogs during walks ($r = -0.33$, $p = 0.02$) and the excitability questionnaire scale scores decreased ($r = -0.32$, $p = 0.03$), older dogs were slower during walks and less excitable in general.
In addition, by using a directional correlation analysis to quantify the fast, joint direction changes of dog pairs we detected that owners had significant role in leading during off-leashed walks and runs, and dogs displayed huge but consistent variability in following the owners.
These findings provide further support for automated animal personality measurements which could be useful in ageing research too. (ERC 680040).

- P32 - CANINE OLFACTORY DETECTION OF LUNG CANCER IN HUMAN URINE: A STEP FORWARD IN DOG LEARNING AND TRAINING

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Highlights:

Volatile organic compounds produced by tumors are released into a patient's breath, sweat and urines. Volatile organic compounds specific odors might be detectable by dogs, due to their exceptional olfactory acuity. This study develops a method for canine olfactory detection of human lung cancer in urine samples. Such approach enables an early diagnosis and consequently a favorable prognosis.

Keywords: *lung cancer; sniffer dog; training; urine sample*

Human lung cancer is the leading cause of cancer-related deaths in the world because early diagnosis is difficult. Three female family dogs (2 Belgian Malinois and 1 mixed-breed dog) aged 2.5–6 yrs are currently being trained by clicker training method (operant conditioning) with positive reinforcement (food) to scent and recognize urine of people with lung cancer (LCa). In this first learning phase, dogs were thought to discriminate between urine from individuals with LCa and urine from healthy controls, both recruited in the European Institute of Oncology (IEO) of Milan. The dogs were thought to signal a cancer urine, by sitting in front of it, among samples containing only one LCa urine and three to five randomly selected controls. Data was analyzed using nonparametric statistics and regression models (SPSS, version 22.0 for Windows; SPSS Inc., Chicago, IL, USA). Dogs showed an increasing trend in the percentage of correct choices across the training period. The factors dog, number of daily session and time of training emerged as robust predictors of a dog's correct choice ($p<0.05$). These findings provide information which are useful in improving rational and effective dog training strategies for olfactory detection of lung cancer on urine samples. Moreover, they would suggest that LCa gives a VOCs-related odor signature to urine. If the next phases of this study confirm these results, then the integration of sniffer dogs into research strategies will turn out to be a useful tool for early diagnosis of lung cancer and improved patient survival.

- P33 - ESTIMATION OF DOG'S OLFACTORY DETECTION THRESHOLD USING SPONTANEOUS SNIFFING BEHAVIOR

A. Concha[1],[2]* (presenting), T. Pike[2], D.S. Mills[2], H. Zulch[2]

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Highlights:

An odor-based paired comparison task was developed and used to estimate spontaneous detection thresholds to amyl acetate in untrained dogs. This method offers a way of comparing olfactory threshold within and between subject without the need for extensive training.

Keywords: *detection thresholds; odor; sniffing behavior; spontaneous*

Olfactory performance in dogs is typically estimated using operant conditioning techniques, but a major disadvantage of this approach is the time required to train a dog before performance can be assessed. A characteristic spontaneous sniffing response is evoked by an odor stimulus even in the absence of training. This spontaneous olfactory detection threshold could be used as a metric for assessing changes in the minimal stimulus concentration detectable by an individual or between individuals. We investigated whether spontaneous sniffing duration in untrained dogs can be used to determine an olfactory detection threshold to amyl acetate using an odor-based paired comparison task (OPCT). Twelve dogs were tested on a range of six different concentrations of amyl acetate. The OPCT consisted of presenting a solvent for familiarization, followed by the presentation of the same solvent paired with a concentration of amyl acetate (novel odor). Using this approach the spontaneous olfactory detection threshold of untrained dogs was determined at 100ppm ($\chi^2(6) = 16.683$, $p < 0.001$) based on changes in sniffing duration. This study provides evidence that the OPCT is a suitable methodology for rapidly assessing a detection threshold based on spontaneous sniffing behavior. Although this is not necessarily a measure of absolute performance threshold limit, this threshold is probably affected by many of the same factors as the actual threshold.

- P34 - AN ANALYSIS OF THE COGNITIVE STRUCTURE OF DOGS: AGE, SEX AND TRAINING EFFECTS

L. Wallis[1],[2]* (presenting), F. Range[1], C.A. Müller[1], S. Serisier[3], L. Huber[1], Z. Virányi[1]

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Highlights:

We tested 145 pet Border collies in the Vienna Canine Cognitive Battery including 11 subtests. Analyses revealed the structure of cognitive abilities & influence of control processes. Age influenced Problem Solving, Dependency, Social Attentiveness, Gaze following, and Exploration. Training influenced Proactivity, Problem Solving, Social Attentiveness, and Persistency.

Keywords: *cognitive battery; cognitive structure; lifespan development; pet dogs; training*

Neither the lifespan development nor the underlying organizational properties of dogs' cognition influencing their trainability, problem solving and learning abilities and interactions with humans have been extensively investigated. We utilized the Vienna Canine Cognitive Battery (VCCB) consisting of 11 subtests to examine correlated individual differences in a set of tasks addressing social, physical, and general cognition, as well as basic control processes (such as attentiveness, dependence, motivation and exploration). In order to avoid variation of data resulting from breed differences, one single breed, the Border collie was used. One hundred and forty-five dogs were divided into seven age groups (from 6 months to 14 years). Seventy-two behavioral variables were coded, and principle component analyses (PCA) were run first at the subtest-level and then on the resulting 27 subtest-level components. The higher-order PCA yielded eight final factors: Proactivity, Problem Solving, Dependency, Social Discrimination, Social Attentiveness, Gaze Following, Exploration, and Persistency. Basic control processes were found to influence cognitive abilities in six of these factors, and the effects of age, training, and sex on the eight factors were also examined. Results revealed significant effects of age on Problem Solving, Dependency, Social Attentiveness, Gaze Following, and Exploration. Training increased Proactivity, Problem Solving, Social Attentiveness, and decreased Persistency. Males showed increased Dependency in comparison to females. The VCCB can be used as a method to quantify lifespan cognition in pet dogs and highlights the influence of training and basic control processes on cognitive abilities.

- P35 - PERCEPTION OF ANIMACY IN DOGS (Canis Familiaris)

J. Abdai[1]* (presenting), C. Baño Terencio[1,2], B. Ferdinandy[3,4], Á. Miklósi[1,4]

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Highlights:

We tested whether dogs similarly to humans can perceive animacy based on simple motion cues. We applied a method that has been successfully used in human infants and adults. Results suggest that dogs perceive interaction between geometric shapes based on their motions.

Keywords: *behaviour; chasing; dog; perceptual animacy; visual perception*

Chasing is one of the most often used movement pattern when investigating perceptual animacy, i.e. observers' tendency to interpret simple motion cues as interactions between objects. Researchers found that young infants prefer to look at a chasing pattern, while older infants and adults tend to look longer an independent movement probably due to the quick recognition of the chasing pattern. Due to general mammalian homology we suggest that dogs may also be able to spontaneously recognize the chasing pattern based on simple motion cues. Here we investigate whether dogs are able to discriminate between chasing and random patterns performed by geometric shapes by using the side-by-side video display of the two stimuli (two trials following each other). We measure dogs' looking duration at the stimuli. We hypothesize that dogs show preference for the chasing in Trial 1, but look longer at the random motion in Trial 2 due to the rapid recognition of the chasing pattern. Results suggest that in Trial 1 dogs look the stimuli equally long; however, they look longer at the independent movement in Trial 2 (GLMM, Trial 1: $F(1,78)=1.76$, $p=0.188$; Trial 2: $F(1,78)=5.09$, $p=0.027$). We also found that dogs look longer the chasing in Trial 1 compared to Trial 2 (Related-Samples Wilcoxon: $N=21$, $Z=-2.21$, $p=0.027$). We suggest that dogs recognize the chasing in Trial 1 and habituate to it rapidly, while they continue to show interest for the independent movement, the "puzzling pattern". Similar result has been found in humans; however, further comparisons are needed.

- P36 - A MULTIVARIATE ANALYSIS OF BEHAVIOURAL SIGNS OF SEPARATION-RELATED PROBLEMS IN DOGS

L.S. de Assis[1]*(presenting), R. Matos[1,2], T. Pike[1], O. Burman[1], D.S. Mills[1]

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Highlights:

Although separation-related problems (SRP) are common in dogs they are still not well defined. We analysed behaviours of dogs showing SRP from a questionnaire to identify their correlations. Six groups with 52 behaviours were most relevant for distinguishing different forms of SRP. These groups represent different motivations and emotions of SRP, improving diagnosis and treatment.

Keywords: *dog behaviour; owner-based questionnaire; separation anxiety*

The main noticeable behaviours of dogs that exhibit separation-related problems (SRP) are destructiveness, vocalization and house soiling when separated from their owners. However, even when occurring together, each of these behaviours might arise from different underlying motivations depending on their precise form and the specific situation in which they occur; i.e. SRP are a heterogeneous phenomenon, but there is a lack of evidence to support this assumption. Hence, the aim of this study was to identify the most relevant groupings of behavioural signs relating to dogs presenting SRP, and their possible interpretations. A large dataset obtained from an online questionnaire (5122 subjects) on SRP was analysed. From the initial 161 behaviours, a principal component analysis with oblique rotation identified 52 items loading distinctly onto six components. These broadly represented: 'destruction of exit points' (13%); 'vocalization when alone and departure-related distress' (11%); 'house-soiling' (10%); 'oral destructiveness' (8%); 'barking versus tail wagging related to intrusion of personal space' (6%); and 'aggressive behaviours when usual expectations are curtailed or denied' (6%). 'Destruction of exit points' and 'oral destructiveness' items are most strongly correlated (0.41) while 'vocalization when alone and departure-related distress' is weakly correlated with all components except 'aggressive behaviours when usual expectations are curtailed or denied'. Other principal components are weakly correlated or show no correlation. This results show groupings of behaviours that might be related to different underlying motivations and emotions, providing the first empirical evidence that SRP are complex and need varying approaches for efficient treatment.

- P37 - CHARACTERIZATION OF TAIL MOVEMENT IN DOMESTIC DOGS

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Highlights:

Case studies of unsuccessful guide dog partnerships investigated the causes of premature retirement. Guide dog partnerships require compatibility between the dog and owner in various areas. In each case the pair were incompatible in one of these areas therefore the partnership broke down. The factors highlighted can be used for future matching of guide dogs and owners.

Keywords: *guide dogs; human-animal bond; human-dog relationships*

In dogs, visual signaling using the tail has been purported to be one of the main communication channels. Although it seems evident that the movement and posture of the tail differs in accordance with context, no empirical research has been conducted to test this assertion. The aim of this study was therefore to characterize dogs' tail posture and movement during different social interactions. Nine dogs were introduced to, and interacted with, different unfamiliar dogs, unfamiliar humans, and unfamiliar inanimate objects. Movement of the tail while interacting with the targets was video-recorded, from both the top and side, and coded to describe its position at each time point. We used Markov models to describe the probability of the tail transitioning between different positions, and from which we could statistically test for differences in movement patterns between interactions with different social targets. The key finding was that tail movement patterns differed significantly between the conditions (permutations-based tests, $p<0.05$); specifically, the movement of the tail was significantly different when dogs interacted with other dogs (during which they exhibited a range of raised and lowered lateral movements), compared to when they interacted with either humans or objects (when lowered lateral movements predominated). This study provides the first evidence showing that dogs move their tails differently when engaging with different targets. Findings from this study provide a significant methodological advance for, and insight into, canine body language.

- P38 - INFLUENCE OF EMOTIONAL CUES ON SOCIAL LEARNING IN DOMESTIC DOGS: PRELIMINARY RESULTS

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Highlights:

We analyzed dogs in a detour task after positive, negative or neutral human emotional display. Matching the demonstrator was more frequent to the left path and may have facilitated learning. The emotional information affected the time dogs used to solve the social learning task. Dogs were significantly slower after watching the negative demonstration.

Keywords: *dogs; emotions; social cognition; social learning*

The ability to acquire information from others can be extremely important especially when an animal is capable to choose appropriately what and whom to copy. We investigated whether emotional cues of a human demonstrator interfere on dogs' social learning. We tested 52 adult family dogs of various breeds in the classic "V" detour task using three distinct experimental phases: pre-test (subjects allowed to solve the task alone); emotional display (dogs watched unfamiliar experimenter behaving in either a positive, negative or neutral way towards the owner); test (experimenter demonstrated the task and subjects were allowed to solve it). Side of demonstration was counterbalanced. We analyzed 20 dogs that were not successful at pre-test and completed the task during testing. The trial duration decreased throughout trials (GLMM: $p<0.0001$) and this correlation was stronger when the demonstration was to the right. Dogs matched the side of demonstration more frequently when choosing the left path (GEE: $p=0.0064$) and took less time to solve the task when choosing left (GLMM: $p=0.0004$), which may indicate that relying on the demonstrator information may facilitate learning. Also, we found a tendency of the emotional cues on the time to solve the task (GLMM: $p=0.0614$): dogs presented to positive display were faster, followed by neutral and negative (a significant difference of time to complete the detour was found between negative and positive valence, GLMM: $P=0.0251$). These results corroborate findings of social referencing in dogs and suggest that emotional cues may interfere on their ability to learn from humans.

- P39 - DOMINANCE RELATIONSHIPS AND ITS CORRELATES IN A CAPTIVE FAMILY PACK OF ARCTIC WOLVES

S. Cafazzo[1,2]* (presenting), M. Lazzaroni[1,2], S. Marshall-Pescini[1,2]

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Highlights:

We investigated social dominance and its correlates in a family pack of 19 Arctic wolves. We found a linear and consistent hierarchy based on the direction of submissive interactions. Dominance relationships seem to be different among sexes and affected by age. Affiliative behaviours appear to be affected by the sex and the dominance between partners.

Keywords: *affiliative relationships; arctic wolves; dominance debate; sex-separated dominance hierarchy; social dominance*

Dominance is one of the most pervasive concepts in the study of wolf social behaviour but recently, it has become intensely debated. For some authors the bonds in wolf families are better described as parent-off-spring relationships and the concept of dominance should be used just to evaluate social dynamics of non-familiar captive packs (e.g. Mech & Cluff, 2010). However, there is a dearth of studies investigating dominance relationships and its correlates in wolf family packs. Here we applied different analytical methods (I&SI and normalized David's scores (NDS)) to agonistic sociomatrices to determine dominance relationships, their consistency and what may affect them, in a captive family pack of 19 Arctic wolves. We detected a linear ($h'=0.56$, $p<0.0001$) and highly consistent (I&SI vs NDS order: $rs=0.97$, $p<0.0001$) hierarchy based on the direction of submissive behaviours. Rank was positively correlated with age ($rs=0.52$, $p=0.02$). However, preliminary models show that, frequency of agonistic (submissive, dominant and aggressive) behaviours were higher between female-female (FF) and male-male (MM) dyads than female-male dyads (GLM: FF-MM $z=-5.17$, $p=0.0000003$: MM-FM $z=-3.06$, $p=0.006$) and sex-separated linear hierarchies showed a stronger linearity than the mixed hierarchy (males: $h'=0.81$, $p=0.0002$; females: $h'=0.78$, $p<0.003$). Affiliative behaviours were more frequently exchanged in FF than MM dyads (GLM: $z=-2.75$, $p=0.02$). Furthermore, affiliative behaviours were directed more often from subordinate to dominant individuals (GLM: $z=-2.05$, $p=0.04$).
Considering the current debate on dominance in wolves, we will discuss the importance of using consistent measures, and including the multiple aspects of dyads' and sex's relationships in the analyses.

References

Mech, L.D., Cluff, H.D., 2010. Prolonged intensive dominance behavior between Gray Wolves, *Canis lupus*. Canadian Field-Naturalist 124(3), 215–218.

- P40 - QUANTIFYING THE DOG-HUMAN BOND: PATTERNS OF BEHAVIOR TOWARDS OWNERS AND STRANGERS ACROSS A STANDARDIZED TEST SEQUENCE

L. Horn[1]* (presenting), C.A. Müller[2], L. Wallis[1,2], F. Range[2], Z. Virányi[2]

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Highlights:

We tested 300 adult pet dogs in an adapted version of Ainsworth's Strange Situation Test. We used quantitative behavioral coding, Factor Analysis and Latent Class Cluster Analysis. Dogs were grouped into four clusters differing in their behavior towards the owner and a stranger. Both similarities and dissimilarities with child-parent attachment patterns are evident.

Keywords: *attachment; cluster analysis; dog-human relationship*

Dogs are able to form uniquely close bonds with their human owners, supposedly resembling the child-parent attachment bond (e.g. separation distress, secure base effect). However, so far it remains unclear whether a quantitative assessment of dogs' interactions with their owners and with strangers can be used to group them into distinct relationship categories, similarly to the attachment patterns identified in human children.
To answer this question we assessed the interactions of 300 adult pet dogs (various pure and mixed breeds, balanced for sex) with their owners and a stranger in a standardized test sequence that was adapted from Ainsworth's Strange Situation Test. We coded various aspects of dogs' behavior relevant to the dog-human bond, which resulted in 16 variables characterizing the dogs' behavior across the test sequence. From these, we extracted five underlying composite variables using Factor Analysis, which explained 66% of the total variation in the sample. To assess whether the dogs can be grouped into distinct categories according to these five factors, we performed Latent Class Cluster Analysis, which resulted in four clusters (86% of dogs could be reliably assigned to one of these). The dogs in the four clusters differed in their behavior towards and security with the owner and the stranger. While age and breed were found to have some effect on cluster membership, sex had no effect.
Our study shows that we can use quantitative measures of dogs' behavior towards their owners and strangers to group them into distinct relationship patterns.

- P41 - MOTION PREDICTION IN DOGS

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Highlights:

We investigated if the violation of expectancy about object's speed of movement modifies dogs' attention. Experiment was conducted with 12 pet dogs that were pre-exposed or not to a congruent moving stimulus. Results suggest that dogs are able to predict the position of a moving object regardless of pre-exposure.

Keywords: *dog; motion prediction; pre-exposure; violation of expectancy*

Being able to predict the future position of a moving object is crucial to hunt a prey and also to communicate and interact with partners. The aim of this study was to investigate a) if the violation of expectancy about movement speed modifies the dogs' attention and b) the effect of previous stimulus exposure. We developed an inferred motion task, using a projected animation and a real 3D barrier, where the dogs' orientation toward a moving stimulus was compared among three different test conditions: anticipated, delayed and congruent reappearance of a ball from behind the barrier. Twelve adult pet dogs were enrolled for the study and were divided between two experimental groups. Dogs of the EXP group were presented with the congruently moving object twice before observing each test condition, while UNEXP dogs were randomly presented with the test stimuli without pre-exposure. The duration of dogs orientation toward the reappearing ball did not differ among test conditions for both UNEXP ($F = 0.25$, $P = 0.78$) and EXP dogs ($F = 0.46$, $P = 0.64$). However, latency to orient toward the reappearing ball was affected by test condition in both UNEXP ($F = 16.7$, $P < 0.001$) and EXP dogs ($F = 6.07$, $P = 0.048$), with a shorter latency for delayed re-appearance of the ball compared to congruent condition (EXP: $P = 0.24$; UNEXP: $P < 0.001$). The results suggest that dogs are able to predict the future position of an object moving with constant speed regardless of pre-exposure.

- P42 - DO LIVESTOCK GUARDINGS DOGS FRIGHTEN WOLVES?

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Highlights:

We studied night interactions between livestock guarding dogs and wolves. Out of 114 video taped sequences, a third included interactions and 100% of the flocks were visited again by wolves within a week. Livestock guarding dogs interact with wolves through agonistic, but also social behaviors and their presence alone does not prevent wolf attacks.

Keywords: *livestock guarding dogs; interactions; wolves*

Since 2010, wolf damages have been increasing in the South of France, despite flocks are protected with livestock guarding dogs (LGDs). Studying their behaviors in front of wolves will help improve their efficiency, which is a conservation issue. Therefore, we studied night interactions between LGDs and wolves with a thermal camera during the summers 2013 – 2015. Out of 114 video taped sequences, a third included interactions with LGDs. In addition to wolf chasing behaviors, we observed close interactions, either consisting of agonistic behaviors, social interactions like sniffing a bitch in heat or play solicitations (elicited from both species) and tolerance behaviors (no reaction from the dog). Hundred percent of the flocks from which wolves were chased off by LGDs were visited again within a week, and in seven cases, an identified wolf pursued by LGDs stayed around the flock or attempted another attack within three hours. Our results show that LGDs can interact with wolves through agonistic, but also social behaviors and that their presence alone does not prevent wolf attacks. This study strongly suggests that wolves do not consider LGDs as a danger to avoid. Consequently, we may improve LGD's selection by including factors like resource holding potential (RHP), motivation and aggressivity towards predators to increase the risk for the wolf when encountering LGDs.

- P43 - PET DOGS BUT NOT SHELTER DOGS PRESENT SOCIAL REFERENCING WITH THEIR HANDLERS

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Highlights:

Pet dogs present social referencing with their owners when facing an unfamiliar person. When the owner moved back, pet dogs looked faster and took more time to approach the stranger. In the same setting, shelter dogs did not synchronized their behaviour on their caregiver's one. Life history and affiliation influence dogs' ability to synchronize their behaviour with humans.

Keywords: *approach paradigm; dog-human interaction; pet dogs; shelter dogs; social referencing*

When confronted with an unfamiliar object, dogs engage in social referencing, i.e. synchronizing their reaction with that of a human handler. Whether they do so when confronted with an unfamiliar person and if the nature of the bond with their handler is at play have not yet been studied yet. We tested the reactions of 72 pet dogs and 30 shelter dogs confronted with an unfamiliar person. The dogs' handlers were instructed to behave in one of three ways towards the stranger: stay still, approach or retreat. All dogs performed referential looks (permutation tests, pet dogs, $Z=-7.35$, $p<0.01$; shelter dogs: $Z=-4.40$, $p<0.01$) and gaze alternations (permutation tests, pet dogs, $Z=-6.79$, $p<0.01$; shelter dogs: $Z=-3.73$, $p<0.01$) between the experimenter and their handlers. However, in the retreat condition, pet dogs looked sooner and took significantly more time before first contact with the stranger compared to the other conditions (Duranton et al., 2016), whereas it was not found between shelter dogs and their handlers (Anovas, $p>0.05$ for all variables). Further, in the retreat condition, pet dogs gazed at the stranger sooner than shelter dogs ($F(1,34)=8.24$, $P<0.01$) and touched the stranger later than shelter dogs ($F(1,34)=3.9$, $p=0.05$) whereas no differences were found for the other conditions. We conclude that when confronted to a stranger, shelter dogs did not present social referencing with their handlers, contrary to pet dogs with their owners. These findings emphasize the importance of life history and of the affiliative link between the humans and the dogs to observe social referencing.

References

Duranton, C., Bedossa, T., Gaunet, F., 2016. When facing an unfamiliar person, pet dogs present social referencing based on their owners' direction of movement alone. Anim Behav 113, 147-156.

- P44 - HOW DO DOG BRAINS PROCESS LIVE HUMAN FACES AND FACE IMAGES- TWO VISUAL fMRI EXPERIMENTS

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Highlights:

We tested awake dogs with fMRI in two visual setups to investigate face processing. We found bilateral activity in anterior and posterior temporal regions for faces. Processing of faces showed left hemisphere bias in contrast to scrambled images. There was no difference in lateralization between live faces and face images.

Keywords: *dog; face processing; fMRI; neuroscience; visual processing*

Dogs are looking at and gaining information from human faces in a variety of contexts. However, the underlying neuronal background of face processing in dogs is unknown. While some studies use face images and others operate with live face stimuli when measuring dogs' capabilities, we do not have information whether they process these in the same way. With two fMRI experiments, we investigated (1) the location of face sensitive areas and (2) how do dogs process live human faces and face images. In study 1 (n=13) we found activity for faces in two regions: a large bilateral cluster extending from the mid-Sylvian gyrus to the mid-ectosylvian gyrus (left: t(12)=7.72, p(corr)=0.001; right: t(12)=6.31, p(corr)=0.06) and a more posterior bilateral cluster within the suprasylvian gyrus(left: t(12)=8.64, p(corr)=0.045; right: t(12)=8.65, p(corr)=0.013). In study 2 (n=11) we investigated whether dogs process live faces and face images similarly. We found a left hemisphere (LH) bias for faces vs. scrambled images (t(10)=3.33, p=0.008), but no lateralization difference between live faces and face images. The LH bias could be a result of higher level familiarity of face images over scrambled images. Based on these results the use of face images instead of live faces in future visual fMRI setups seems a viable alternative in case of dogs, too. The described face-responsive regions can serve as a basis for further investigations, to find out whether their sensitivity extends to conspecific faces.

- P45 - A QUALITATIVE STUDY ON THE IMPACT OF PREMATURE RETIREMENT OF GUIDE DOGS ON OWNERS

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Highlights:

Interviews with guide dog owners explored the impact their dog's premature retirement had on them. Owners had a complex relationship with their dog, divided by the work and pet relationship. Owners grieved over the loss of the relationship they had with the dog as a pet. Their well-being was impacted as a result of the emotional and physical impact of the retirement.

Keywords: *bereavement; guide dogs; human-animal bond*

Guide dogs assist visually impaired individuals with their mobility as well as conferring social and psychological benefits to the owner (Sanders, 2000). Whilst a guide dog typically works for five to six years (Guide Dogs, 2016), some are retired prematurely for health or behavioural reasons. Research suggests premature retirement may be distressing for the owner (Nicholson et al., 1995). This research explores, from the owner's perspective the experiences of premature retirement of a guide dog with an aim to gain insights into the effect this has on guide dog owners. Semi-structured interviews were conducted with thirteen visually impaired people that had experienced premature retirement of a guide dog. Thematic analysis identified three common themes across participants. The first theme, 'Owner-Dog Relationship' describes the relationship the owners had with their dog, with a clear distinction between the working relationship and the dog as a pet. The second theme was 'Loss', whereby participants described grieving the loss of the dog as a pet from their lives. The final theme was 'well-being' focusing on how the retirement affected their emotional and physical health. The importance of both the working relationship as well as the personal bond with the dog in the success of a guide dog partnership is illustrated by the findings from this study. These findings may help with future matching of guide dog partnerships and could also be applied to other assistance dogs and matching dogs from animal shelters to new homes.

References

Guide Dogs, 2016. Guide Dogs UK Charity For The Blind And Partially Sighted. www.guidedogs.org.uk (Accessed 3rd February 2016).

Nicholson, J., Kemp-Wheeler, S., Griffiths, D., 1995. Distress arising from the end of a guide dog partnership. Anthrozoös 8, 100-110.

Sanders, C.R., 2000. The impact of guide dogs on the identity of people with visual impairments. Anthrozoös 13, 131-139.

- P46 - EVIDENCE FOR SYCHRONIZATION OF STRESS HORMONES IN OWNERS AND DOGS DURING THE STRANGE SITUATION TEST

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Highlights:

Salivary cortisol and chromogranin A were obtained from dogs and owners in the Strange Situation Test. Initial and final values of cortisol and chromogranin A correlated for owners and for dogs. Dog and owner final cortisol, as well as dog final chromogranin A and owner cortisol were significantly correlated. When dogs and owners are faced with a challenge, hormonal synchronization may occur.

Keywords: *chromongranin A; cortisol; dog-owner hormonal synchrony*

Dogs and their owners (N=26) participated in a Strange Situation Test (SST) that involved a series of separation and reuniting events in a novel room, and the presentation of a stranger to the dog. Prior to and following the SST, saliva samples were obtained from dogs and owners, and were analyzed for cortisol (CORT), a glucocorticoid hormone governed by the HPA axis, and chromogranin A (CgA), an analyte purported to reflect sympathetic nervous system (SNS) activation (Obiyahsi, 2013), but not yet well-studied in dogs. Initial and final CORT values were strongly correlated for both dogs ($r=0.75$, $p<0.001$) and owners ($r=0.85$, $p<0.001$). Approximately half of the dogs showed a CORT increase over the SST, and the remainder a decrease. Owner CORT significantly decreased ($t(25)=5.36$, $p<0.001$). Initial and final CgA levels correlated strongly for owners ($r=0.87$, $p<0.001$), but only marginally for dogs ($r=0.54$, $p=0.06$), likely due to reduced CgA sample size. Dogs, but not their owners, experienced a significant decrease in CgA concentrations over the SST ($t(12)=6.8$, $p<0.001$). Dog and owner final CORT concentrations at the end of the SST correlated significantly ($r=0.56$, $p=0.01$), possibly indicating hormonal synchrony in the face of an environmental stressor (SST). Dog final CgA levels were related to their owner's initial and final CORT, but only when dogs without separation anxiety were analyzed ($r=0.84$, $p<0.001$; $r=0.75$, $p<0.001$, respectively). These data add to the small number of studies examining interspecific physiological relationships, and suggest that dog-owner biobehavioural synchronization merits further investigation.

References

Obiyahsi, K., 2013. Salivary mental stress proteins. Clinica Chimica Acta 425, 196-201.

- P47 - RAPAMYCIN AS A POTENTIAL MODULATOR OF AGING IN DOGS: A PILOT STUDY

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Highlights:

Rapamycin increases lifespan in several model organisms, including yeast, worms, flies, and mice. In addition, short-term rapamycin treatment improves cardiac and immune function in aged mice. We tested the safety and efficacy of rapamycin vs. placebo in privately owned middle-aged dogs. Our findings support its safety and indicate that its known cardiac benefits may also apply to dogs.

Keywords: *animal models; aging; drug safety; placebo-controlled clinical trial; rapamycin*

Rapamycin is an FDA approved immune modulator that also shows potent anti-aging effects in model organisms: In middle-aged mice, rapamycin improves cardiac and immune function, reduces cancer rates, delays cognitive decline, and increases lifespan. However, all studies on these effects have thus far been conducted under laboratory conditions rather than under circumstances resembling the human environment. We suggest that the privately owned domestic dog is a uniquely suited model because dogs share our environment, receive comparable medical care, and develop many analogous age-related diseases. Improving healthy aging in dogs will also positively affect quality of life in both dogs and their owners.
Our goal was to establish the clinical safety and begin to assess the efficacy of rapamycin in healthy middle-aged dogs. We recruited more than 40 privately owned dogs over age 6 and weighing over 18 kg into a 10 week double-blind, randomized, placebo-controlled study. Of those, 23 healthy dogs were randomized into either placebo or one of two treatment groups. These received 0.05 or 0.1 mg/kg rapamycin orally 3 times per week.
Blood samples were collected at the beginning and end of the study period, and cardiac ultrasonography performed. We found no significant changes in blood parameters and no significant clinical side effects over the study period. As in mice, left ventricular output was improved in the dogs given rapamycin relative to placebo. Our findings support the safety of rapamycin in healthy middle-aged dogs and indicate that its known benefits for aging may also apply to this species.

- P48 - TESTING INEQUITY AVERSION IN WOLVES AND DOGS

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Highlights:

A test to induce inequity between two conspecific partners was run with 10 wolves and 10 pack-living dogs. Responses in the test conditions were compared to those in multiple controls to determine the existence of an inequity aversion response in both wolves and pack-living dogs. Similarities and differences between the two groups were then compared.

Keywords: *domestic dogs; inequity aversion; wolves*

Inequity aversion refers to an individual responding negatively when its conspecific partner receives a more highly valued compensation compared to what they have received for the same action. Studies show that domestic dogs are inequity averse (Range et al., 2009; Range et al., 2012). It is unclear whether this is an effect of domestication and/or socialization, or whether it was already present in wolves. As inequity aversion is likely linked to cooperation, it is possible that wolves also show this response. In this study, we tested wolves that engage in high levels of cooperation both in the foraging and parental context, and pack-living dogs that have been domesticated by humans, and no longer depend to the same degree on intraspecific cooperation. We tested wolves and domestic dogs raised and kept in the same conditions. In our task, an experimenter alternated between asking two subjects to press a buzzer in exchange for a reward, while the reward given varied depending on the condition. Preliminary results indicate that both dogs and wolves react to being treated unequally. In the inequity condition, when the subject received no reward but the partner did, participants stopped participating earlier than in the equity condition when both subjects were rewarded equally (dogs, T=-2.805, p=0.005; wolves, T=-2.201, p=0.028). However, this effect did not emerge when subjects received a lower quality reward compared to their partner (dogs, T=-1.342, p=0.18; wolves, T=-1.342, p=0.180). Differences in the inequity aversion response according to species, rank distances, and affiliation scores will be assessed.

References

Range, F., Horn, L., Virányi, Z., Huber, L., 2009. The absence of reward induces inequity aversion in dogs. PNAS 106(1), 340-345.

Range, F., Leitner, K., Virányi, Z., 2012. The influence of the relationship and motivation on inequity aversion in dogs. Social Justice Research 25(2), 170-194.

- P49 - IDENTIFICATION OF FEAR BEHAVIORS SHOWN BY PUPPIES IN RESPONSE TO NOVEL OBJECTS

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Highlights:

A test was administered to 21 puppies to determine what behaviors are associated with fear. Trials (N=163) were scored for fearfulness, and duration and frequency of behaviors were recorded. Lowered posture and tail, freezing, flinching, lip licking and barking were found to be associated with fear. Reduced environmental interactions, locomotion and panting were also associated with fear.

Keywords: *canine behavior; development; fear; puppy*

Fear behaviors in puppies have not been properly identified, and it is unknown whether they are similar to behaviors seen in older dogs. We assessed which puppy behaviors are associated with fear of a novel object. Puppies (<6 months; N=21) were introduced into a 3.5 meter long run and trained to approach the far end to obtain a food reward. After training, each puppy completed four trials with noisy or unpredictable novel objects and four with no objects (control). All sessions were video-recorded, and behavior during each trial (N=163) was scored using Noldus Observer 12. Trials were categorized as 'fearful' if the puppy did not approach the end of the run, or the latency to approach was greater than the mean+2 SD of the control trials. Linear, logistic and Poisson mixed models, with puppy as a random effect, were used to model behavior durations, presence (yes/no), and counts, respectively. The following behaviors occurred more in 'fearful' trials in comparison to control trials: lowered posture ($p<0.001$), lowered tail ($p=0.003$), freezing ($p<0.001$), flinching ($p=0.001$), lip licking ($p=0.011$) and barking ($p=0.001$). Interactions with the environment (scratching/sniffing; $p<0.001$), locomotion ($p<0.001$) and panting ($p=0.011$) occurred less in 'fearful' trials. No significant difference was found for tail wagging. Yawning, shaking, paw lifts, elimination, whining and growling occurred too infrequently for analysis. These results indicate that postural, lip licking and barking behaviors are the most reliable indicators of fear in puppies in situations where they are able to control their approach to objects that elicit fear.

- P50 - DOG LOVER DEDICATION: THE GOOD, THE BAD AND THE TRUE LOVE WAYS OF THE HUMAN-CANINE RELATIONSHIP

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Highlights:

Dedicated dog owners were questioned about their activities, emotions and difficulties with their dog. Owners perceived that their dogs reacted to their emotions and displayed a variety of similar emotions. Few difficulties impacted on their human-canine relationship with an overwhelming majority of owners expressing love for their dog.

Keywords: *dogs; dog owners; human-canine relationship; survey*

Dog owners are often highly attached to their pet and involve their canine companion in many aspects of their life. They may also be very attuned to their dog's emotions and perceive that their dog reacts to their human emotions. The human-canine relationship, however, may be negatively impacted by factors such as health, behaviour, and relationship breakdown. Knowledge of the dedicated dog owner's commitment may improve our understanding of those less involved dog owners.
A survey was conducted on 800+ dog owners, specifically targeting those who considered themselves dedicated owners, on practical and emotional aspects of the human-canine relationship. Dog owners were asked about their canine activities, both within and outside of the home and about their emotional relationship with their dog. Factors affecting their relationship were identified and owners were also asked about improving their relationship with their dogs.
Few factors negatively impact the dedicated dog owner's relationship with their dog. Many owners would not change anything about their dog, given the chance, although some did experience behaviour issues with their dog and this was identified as an area owners wished to learn more about. More than half of respondents, however, considered themselves to be very knowledgeable on dogs.
Most owners perceived that their dog responded to their human emotions and that their dog displayed emotions of happiness, love, fear and jealousy. The majority of survey respondents claimed to love their dog and believed that their dog loved them back.

- P51 - COMPARING MOTOR BIAS IN DOGS AND HUMANS

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Highlights:

Forelimb use on a comparable retrieval task was assessed in humans and dogs**.** Humans used their non-dominant hand to stabilise a ball**.** Dogs showed a preferred paw for performing a similar task. Dogs, like humans, may be using their non-dominant limb on the Kong ball test.

Keywords: *domestic dog; handedness; laterality; Kong ball; welfare*

The Kong ball test has been used extensively to assess lateral asymmetry in the domestic dog. Here, the paw used to stabilise a food-filled ball is recorded. Implicit in this challenge is the assumption that dogs use their dominant paw to stabilise the ball. This study examined whether or not this is the case. A comparative approach was adopted. In Experiment 1, the paw preference of 48 pet dogs was assessed on the Kong ball test. Significantly more dogs were paw-preferent than ambilateral (P=0.01, binomial test). There was no significant difference in the number of dogs that were right- vs. left-paw preferent (P=1.00, binomial test). In Experiment 2, 94 adult humans were assessed on their ability to remove a piece of paper from a Kong ball with their mouth, using their left or right hand to stabilise the ball. Participants completed the Edinburgh Handedness Inventory Short Form to assess their handedness quotient (HQ). Analysis revealed a highly significant association between HQ and the hand used to stabilise the Kong ball (Chi-squared=31.31, df=1, P<0.001). Most of the left-handed individuals (82%) used their right hand to stabilise the ball, while the majority of the right-handed participants (76%) employed their left hand to perform the feat. The findings point to the strong possibility that dogs, like humans, employ their non-dominant paw to stabilise the Kong ball, and use their dominant side for postural support. These results have implications for work attempting to relate directional motor bias to emotional functioning and welfare risk.

- P52 - INVESTIGATING EMPATHY-LIKE RESPONDING TO CONSPECIFICS' DISTRESS IN PET DOGS

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Highlights:

The study investigates whether dogs would show empathic responses to conspecifics' distress. Subjects were first exposed to a playback phase. In this phase, a control sound, a familiar whine or a stranger whine was played back. Then in a reunion phase the familiar partner dog entered the room.
Results showed that dogs can demonstrate "empathic-like" responses to conspecifics' distress-calls.

Keywords: *dogs; emotional contagion; empathy; sympathetic concern; whines*

While most studies about empathy have investigated how animals reacted in response to conspecifics' distress, dogs have mainly been targeted to examine their empathic responses towards humans. To investigate whether dogs would show empathic responses also to conspecifics, we adopted a playback method using conspecifics' vocalizations (whines) recorded during a distressful event as well as control sounds. Our subjects were first exposed to a playback phase where they were subjected either to a control sound, a familiar whine or a stranger whine stimulus, and then a reunion phase where the familiar partner entered the room. When exposed to whines, dogs exhibited a higher behavioral alertness ($F_{(1, 29)} = 10.08$, $p=0.003$) and stress-related behaviors ($F_{(1,29)} = 5.247$, $p = 0.03$) compared to when exposed to acoustically similar control sounds. Moreover, they demonstrated more comfort-offering behaviors toward their familiar partners following whine playbacks than after control stimuli ($F_{(1, 31)} = 7.685$, $p = 0.009$). Furthermore, when looking at the first session, this comfort offering was biased towards the familiar partner when subjects were previously exposed to the familiar compared to the stranger whines ($F_{(2, 13)} = 8.31$, $p = 0.005$). Finally, familiar whine stimuli tended to result in higher cortisol levels while stranger whines did not ($F_{(1, 6.09)} = 4.66$, $p = 0.07$). To our knowledge, these results are the first to suggest that dogs can experience and demonstrate "empathic-like" responses to conspecifics' distress-calls.

- P53 - ANALYSIS OF CORRELATIONS BETWEEN EARLY SOCIALIZATION AND AGGRESSION IN THE DOG

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Highlights:

A retrospective questionnaire of 783 dog owners found that many socialized their puppy in public prior to onset of vaccine immunity. Around one third of owners reported that their dog has displayed aggression towards other dogs. Puppies socialized in public earlier had higher odds of being aggressive to dogs. Intensity of puppy socialization not correlated with risk of inter-dog aggression.

Keywords: *dog aggression; public socialization; puppy socialization; vaccination*

It is believed that socialization of puppies is required to prevent later aggression. However, socialization of puppies in public areas is unsafe prior to the onset of immunity of the primary vaccination course (usually at 16-18 weeks). A retrospective questionnaire completed by 783 Australian participants was used to quantify the amount and age of early socialization experience of pet dogs. All dogs were currently between 1 and 3 years of age, acquired before 10 weeks of age, and from a variety of breeds. Participants reported the age at which they first took their puppy into public areas such as the sidewalk, beach and parks. They then quantified the intensity of socialization their puppy received. Finally, owners answered whether their dog ever displayed aggressive behaviour to unfamiliar dogs. 51.6% (95%CI = 48.0-55.1) of puppies began public socialization prior to the final vaccination of their primary immunization course. In 34.1% (95%CI = 30.8-37.5) of responses, participants reported that they had previously seen their dog display aggression towards an unfamiliar dog. Logistic regression modelling found that every week that an owner waited to begin public socialization reduced the odds of their dog becoming aggressive as an adult by 4.2% (95%CI 0.2-7.9, P = 0.041). Intensity of socialization was not correlated with risk of inter-dog aggression ($P > 0.2$). These results suggest that some experiences occurring with young puppies in public may predispose them to later aggression and therefore more emphasis should be placed on safer alternatives like supervised private socialization classes.

- P54 - REMOTE THERMOGRAPHIC MONITORING OF EAR TEMPERATURE IN RELATION TO SEPARATION STRESS IN DOGS

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Highlights:

Pet dogs were tested in a brief separation test and filmed remotely using thermography. Images of both ears were analysed for median temperature over a standard ear patch. Social isolation was associated with a significant decrease in ear pinnae temperature. Long distance thermography is a useful tool in non-invasive stress monitoring.

Keywords: *Canis familiaris; dogs; infrared thermography; non-invasive stress monitoring; separation related problems*

The potential of infrared thermography for remote stress monitoring was explored in pet dogs, with a focus on changes in temperature of the ear pinnae. Six dogs were tested in a separation test in which they received contact with their owner, a stranger, or were left alone in an unfamiliar room. Three of the subjects were reported to exhibit separation-related problems; the other three dogs did not. Tests were filmed using a FLIR T420 thermographic camera positioned in the room corner (thus there was no need for human presence). Effects of different social conditions on ear pinnae temperature were assessed using GLMM. For both groups of dogs, temperature of both ear pinnae decreased significantly during separation and increased significantly when a person (either the owner or a stranger) was present (all $p<0.05$), with no significant difference between situations involving the owner or the stranger ($p>0.05$). This indicates that separation stress is associated with an immediate reduction in ear temperature, and that isolation in the unfamiliar environment constituted a stressful experience also for dogs not normally suffering from separation related problems. The pattern of ear temperature changes observed in the current study was largely paralleled by dogs' heart rate patterns in two studies on dogs' cardiac responses to social contact and isolation, which supports the validity of the methodology in the non-invasive assessment of stress in animals. This is the first study using 'long distance' measurement of body surface temperature for gauging physiological stress responses.

- P55 - TRAINING DOGS FOR ACCURATE EYE-TRACKING

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Highlights:

We use a high-end eye-tracking system to investigate pet dogs' visual perception. We developed a training procedure to get reliable and accurate eye-tracking results. So far we successfully trained 40 pet dogs and conducted 6 eye-tracking experiments.

Keywords: *domestic dogs; eye-tracking; positive reinforcement; training*

Eye-tracking is an attractive tool to examine how humans and animals process visual stimuli (pictures, videos, live demonstrations). Tracking details of others' gazing patterns helps us reveal the cognitive mechanisms underlying these processes in other species. However, most eye-tracking systems have been developed for recording human eye movements and critical parts of the experimental procedures rely on verbal communication with the subjects; e.g. precise calibration is ensured by asking adults to look at the calibration dots and verbally rechecking. Since this is not possible with animals, we developed a training procedure to prepare dogs for accurate eye-tracking, enabled by using a high-end eye-tracking system, Eyelink1000.
This training aimed at gaining a behavioral response of dogs that can replace verbal feedback and keeping dogs motionless to enable longer term eye-tracking. The training consisted of 3 phases: 1) chin rest training: the dogs learn to stay laying their head on a chin rest in front of the eye-tracker, 2) black dummy screen training: the dogs learn to look at a moving light dot on the screen and to touch it with their nose, 3) calibration training: combines staying in the chin rest and looking at the dots. So far we have trained 40 dogs (25 females, 15 males, age range: 7 months to 10 years, various breeds of pet dogs). The training lasted for at least two months (range: 8 to 30 weeks) with each of them. Since then all dogs have successfully participated in 2 to 6 eye-tracking experiments.

- P56 - RECOGNITION OF LIVE HUMAN FACES BY PET DOGS

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Highlights:

Pet dogs were assessed on their ability to recognize their owners' faces. Owners' and strangers' faces were presented with peculiar orientation, lighting and covered hair. Dogs chose the owner only when viewed frontally, with visible hair and no spotlight. Dogs' use of visual information in recognition of humans' faces is questioned.

Keywords: *dog; human face; owner; recognition*

Several studies have focused on how dogs use visual information about human faces, but their ability to recognize the faces of familiar people is not yet understood. We tested 30 dogs on their ability to recognize their owners by using face information alone. In a series of two-choice tasks, dogs had to choose between their owner and a stranger, who wore identical clothes and stood behind an apparatus that allowed dogs to only see the people's legs and heads. In the TEST condition heads were not frontally oriented towards the dog and were illuminated by a spotlight, while a shower cap covered the people's hair. In the BASE condition, heads faced the dog, there was no spotlight and no cap. In the ODOR condition, only legs were visible. A choice was recorded when the dog overstepped the apparatus where one of the two people stood. Only in BASE condition the dogs choose the owner above chance (N = 22, P = 0.008, one-tailed Binomial). Condition had a significant effect on choices (Q = 6.7, P = 0.03), as dogs chose the owner more often in BASE than TEST (N = 14, Q = 5.3, P 0.02) and ODOR (N = 15, Q = 5.4, P 0.02), whereas no difference was found between the latter two (Q = 0.07, P = 0.7). Results suggest that dogs cannot recognize their owner's face under certain viewing conditions, raising questions about which perceptual information is most relevant for human face recognition by dogs.

- P57 - THE AIMS OF PRE-ADOPTION DOG ASSESSMENTS CONDUCTED BY REHOMING ORGANIZATIONS IN THE UK AND US

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Highlights:

Organizations were asked what information they sought from pre-adoption dog assessments. A thematic qualitative analysis was conducted on the data provided. There were consistencies in the types of information sought between organizations. Aggression was the most common factor that would deem a dog unadoptable.

Keywords: *adoption; assessment; dog; rehoming*

Millions of dogs globally enter animal shelters every year, and decisions made about their behavior and rehoming potential can have significant consequences. Many studies have examined the use of behavioral tests to assist such decision-making. However, substantially less scientific attention has been paid to the types of information that organizations seek to gain from these tests. In order to carry out such an analysis, 515 rehoming organizations, including local branches, were contacted in the UK and US. They were asked open-ended questions relating to their formal or informal assessments, including what characteristics of the dog they are aiming to find out about, if any aspects of the assessment are given more weight than others, and if any results from the assessment would deem a dog unadoptable. Organizations were requested to provide a copy of any form or document that is completed as part of their assessment. A thematic qualitative analysis was conducted on the responses to the written enquiry and on any supplemental documentation provided. The amount of information provided by respondents varied widely, but there were consistencies in the types of behavioral information sought. Not all organizations stated that they have criteria that would deem a dog unadoptable, but for those that did, aggression was the most common factor. The findings of this research highlight the importance of behavior in pre-adoption screening, and the need for reliable and valid tests that predict these traits.

- P58 - THE EFFECT OF REWARD-HANDLER DISSOCIATION ON DOGS' OBEDIENCE PERFORMANCE IN DIFFERENT CONDITIONS

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Highlights:

We examined the effect of reward-handler dissociation on dogs' obedience in different conditions. Food reward for good performance was provided either by the handler of by a dispenser device. Obedience decreased with increasing distance from the handler. Reward-handler dissociation affected dogs' obedience in distant conditions.

Keywords: *behaviour; dog; food reward; obedience; training*

Dogs' responsiveness to instructions of the handler is influenced by several factors. We examined whether reward-handler dissociation affects the obedience performance of family dogs with basic training history (N=30). We measured dogs' obedience performance to commands ('sit' and 'down') under controlled laboratory settings. For two different groups we manipulated the source of the food reward: it was provided either by the handler or by a remote controlled food dispenser device during a practising period, when the handler stood in the dog's close vicinity (0.5 m). In three different test conditions the position of the handler was manipulated: he/she stood further away (3 m) from the dog either beside a screen, behind the screen or outside of the room. No food reward was provided during the test trials. We found that the performance of dogs that experienced receiving food reward from the handler was significantly poorer during the test conditions, i.e. in contexts with increased distance between them and the handler (including handler out of sight), as compared to their performance during the reminder sessions in the handlers' close vicinity (GLMM, χ^2_1=10.38, p=0.001) Experience with receiving food reward form the dispenser device lessened the difference in dogs' obedience between the test conditions and reminder sessions (GLMM, χ^2_1=3.01, p =0.083), and moreover, it also revealed a more prompt response to the 'sit' than to the 'down' commands (GLMM, χ^2_1=9.94, p =0.002). Thus our results show that reward-handler dissociation seems to affect dogs' obedience performance in the investigated conditions (Gerencsér et al., 2016).

References

Gerencsér, L., Kosztolányi, A., Delanoeije, J., Miklósi, Á., 2016. The effect of reward-handler dissociation on dogs' obedience performance in different conditions. Appl Anim Behav Sci 174, 103-110.

- P59 - THE FUNCTION OF OPPONENTS AND BYSTANDER POST-CONFLICT AFFILIATIVE INTERACTIONS IN A CAPTIVE FAMILY PACK OF ARCTIC WOLVES

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Highlights:

A study on the function of affiliative post-conflict interactions was carried out on a family pack of captive Arctic wolves. It seems that the function of these interactions is to reduce the frequency of further aggressions.

Keywords: *affiliative relationships; arctic wolves; bystander post-conflict affiliation; dominance relationships; reconciliation*

Post-conflict Affiliative Interactions between opponents (PAI or 'reconciliation') and Bystander Post-conflict Affiliative Interactions between a bystander and a victim of an aggression (BPAI) have been extensively studied in primates but only superficially in other mammals.
In wolves only few studies used the post-conflict (PC)/matched control (MC) method and found both PAI and BPAI more in PCs than MCs, concluding that affiliative post conflict interactions occur (e.g. Palagi & Cordoni, 2009). However, the function of these interactions is still not clear. We tested the function of both PAI and BPAI in a captive family pack of 19 Arctic wolves. Using independent measures of dyadic rank and affiliative relationships, we investigated whether these factors affect the occurrence of PAI and BPAI.
Preliminary results show that PAI occurred sooner in PCs than MCs (Wilcoxon: $z=6.5$, $p<0.001$) and were more likely to be initiated by the victim (Mann-Whitney: $z=2.18$, $p=0.03$). PAI reduced the likelihood of re-aggression (glmm: $z=3.2$, $p=0.002$) and re-directed aggression (glmm: $z=2.65$, $p=0.01$). Affiliation did not affect the likelihood of PAI occurring.
BPAI occurred sooner in PCs than MCs (Wilcoxon: $z=7.87$, $p<0.001$) and were as likely to be initiated by the victim than the bystander. BPAI reduced the likelihood of re-directed aggression (glmm: $z=3.99$, $p=0.0002$) and of bystander aggressions on the victim (glmm: $z=3.85$, $p=0.0003$). BPAI occurred more often between individuals with a high affiliative score (glmm: $z=2.88$, $p=0.006$).
We discuss these results in light of current knowledge of post-conflict behaviour.

References

Palagi, E., Cordoni, G., 2009. Postconflict third-party affiliation in *Canis lupus*: do wolves share similarities with the great apes? Anim Behav 78, 979-986.

- P60 - DO FREE-RANGING AND PET DOGS DIFFER IN THEIR PROBLEM-SOLVING ABILITIES AND HUMAN-DIRECTED BEHAVIOUR?

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Highlights:

Free-ranging dogs from India and pet dogs from Vienna were tested in the "unsolvable task" paradigm. Free-ranging dogs were slower in solvable trials, but as persistent as pets in the unsolvable one. They had different human-directed behaviour suggesting that socialization has a strong effect on it.

Keywords: *free ranging dogs; human directed behaviour; persistence; problem solving*

Dogs inhabit a wide variety of environments – from comfortable sofas of loving families to the harsh roads of cities. Yet, behavioural and cognitive research has mostly focused on studying pets whose socialization and selection for specific working roles might make them different from other dog populations. Here we asked how similarly pet dogs and free ranging dogs behave in a socio-cognitive task. Using the "unsolvable task" paradigm we tested 21 free-ranging dogs on the street in India and 17 mixed-breed pets in dog walking areas in Vienna to compare their persistence (e.g. duration of interacting with the apparatus) and human directed behaviour (e.g. gazing at a human). Preliminary analyses show that in the first, solvable trial, free-ranging dogs were more persistent than pets (LM, $t=3.38$, $p<0.001$) and more persistent dogs from both groups looked at a human more frequently (GLM, $z=9.4$, $p=0.003$). Controlling for persistence, free-ranging dogs looked back more than pets (GLM, $z=4.47$, $p<0.001$) and were slower at obtaining the food (LM, $t=3.62$, $p<0.001$). In the unsolvable trial, dogs in both groups were equally persistent (LM, $t=58$, $p=0.56$), and more persistent dogs tended to look back later (LM, $F=3.78$, $p=0.059$) and less frequently (GLM, $Chi^2=16.36$, $p<0.001$). Controlling for persistence, pets looked back more frequently (GLM, $z=3.9$, $p<0.048$) than free-ranging dogs. These results suggest that free-ranging dogs behave differently from pets and since they show the greatest genetic variability and represent 70-80% of the world's dog population, should be included in studies on dog behaviour and cognition.

- P61 - DO DOMESTIC DOGS PERCEIVE THE DELBOEUF ILLUSION?

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Highlights:

Visual illusions are commonly used as a tool to compare visual perception among vertebrates. We investigated Delboeuf illusion using a free choice test recently adopted with chimpanzees. Dogs were accurate in the control task, while no evidence of Delboeuf illusion was found. This suggests a discontinuity between dogs and primates in perceptual biases affecting size judgments.

Keywords: *Canis lupus familiaris; comparative perception; optical illusions*

The issue of how nonhuman animals see the world has interested philosophers and scientists from ancient times. In the last decades it has become more common to use visual illusions as a tool to compare the visual perception among the species. In the present study we investigated whether domestic dogs perceive the Delboeuf illusion. This illusion determines a misperception of item size as a function of its surrounding context. For instance, when a larger concentric dot encompasses another dot, this latter dot is generally perceived to be smaller than when it is encircled by a relatively smaller concentric dot.
We used a free choice test similar to that recently used to investigate the same issue in chimpanzees. In control trials, two different amounts of food were presented in two identical plates and dogs were expected to select the larger amount. In test trials, two identical amounts of food were presented in two plates differing in size: if dogs perceive the size illusion, they were expected to select the amount of food presented in the smaller plate.
Results showed that dogs were accurate in control trials ($t(12) = 6.289$, $p < 0.001$) while their performance did not differ from chance in test trials with the illusory pattern ($t(12) = 1.737$, $p = 0.108$). On the whole, no evidence for Delboeuf illusion in domestic dogs was found, suggesting a potential discontinuity in the perceptual biases affecting size judgments between primates and dogs.

- P62 - WHO WILL BE MY HELPER?

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Highlights:

Dogs witnessed a human partner who was skilled in problem-solving and another who was unskilled. Referential looks to the humans in an unsolvable task were then used to assess reputation formation. Looks' frequencies, durations and first choice suggest that dogs did not differentiate the partners. Dogs might not evaluate humans based on skillfulness, or use the information in this context.

Keywords: *dog; help-requesting; problem-solving; referential looking; reputation*

Reputation formation is crucial for social, and especially cooperative, interactions. Dogs evaluate humans based on direct experience (Nitzschner et al., 2012) and, possibly also based on indirect experience (Chijiiwa et al., 2015). This has been mainly tested in contexts where humans were either nice or not towards others. In the current study we investigated reputation formation based on seeing human partners being skilled or unskilled. Thirty-two adult pet dogs observed 4 blocks of 2 demonstration types. A skillful experimenter succeeded in solving a puzzle and obtaining food for the dog. An unskillful experimenter failed, though food was dropped inconspicuously. Blocks were followed by "unsolvable problem" trials: dogs were presented with a container baited with food that was inaccessible, while the experimenters stood either side of it. Referential looks towards each experimenter were recorded.
Dogs who looked referentially (N = 31) did not look at the skillful experimenter first above chance (Wilcoxon signed-rank test: Mdn = .50, T = 147, p = .31, r = - .18). There was also no overall difference between the frequencies of looks at the skillful vs the unskillful experimenter (Wilcoxon signed-rank test: $Mdn_{Skillful}$ = 2.25, $Mdn_{Unskillful}$ = 2.00, T = 199.00, p = .81, r = .03) or their duration ($Mdn_{Skillful}$ = 2.37, $Mdn_{Unskillful}$ = 2.35, T = 261.50, p = .37, r = .03). These results suggest that dogs might not take into account skillfulness when looking referentially at humans for help, or possibly could not use the information to evaluate them in this context.

References

Chijiiwa, H., Kuroshima, H., Hori, Y., Anderson, J.R., Fujita, K., 2015. Dogs avoid people who behave negatively to their owner: third-party affective evaluation. Anim Behav 106, 123-127.

Nitzschner, M., Melis, A.P., Kaminski, J., Tomasello, M., 2012. Dogs (*Canis familiaris*) evaluate humans on the basis of direct experiences only. PLOS One 7, e46880.

- P63 - ATTRIBUTION OF EMOTION TO DOGS

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Highlights:

Exploratory factor analysis was conducted on a 12-item scale measuring attribution of cognitive and emotional characteristics to dogs. Four factors were extracted that explained 65% of the variance. The ability to measure these attributions is important in understanding the effect of misattributions and anthropomorphism on animal welfare.

Keywords: *anthropomorphism; cognitive attribution; factor analysis; human-canine bond; scale development*

Humans have a tendency to anthropomorphize. Our anthropomorphic tendencies may lead us to believe that certain dog behaviors are more cognitively complex than they are. For example, owners sometimes assume that dogs have a complex theory of mind, understand aspects of human morality and exhibit guilt and deceit. These possible misattributions have implications for animal welfare, as assumptions about motivations (e.g. guilt, deceit) may lead to punitive and inappropriate responses in the human. The first step in studying cognitive attributions is to develop a valid and reliable measurement scale. This study is an initial attempt to develop such a scale. Ninety-three students and faculty members from two college campuses completed the survey and the Lexington Attachment to Pets Scale (LAPS) as part of a larger research study. A principal components analysis with varimax rotation was conducted. The Scree test and the eigenvalues-greater-than-1 rule both support the extraction of 4 factors: Understanding human emotion, Negative emotional motivation, Positive emotional motivation, and Human-Canine Bond. All four factors were significantly correlated with the LAPS, suggesting that those who are most attached to their pets may also have significant misunderstandings of canine cognition and emotion.

- P64 - USE OF PREFERENCE ASSESSMENTS AND STRUCTURED POTENTIAL ADOPTER-DOG INTERACTIONS INCREASES ADOPTIONS

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Highlights:

A behavioral intervention was developed to increase adoption rates of shelter dogs. A brief play preference assessment for shelter dogs was first developed and validated. Data from 160 interactions between potential adopters and dogs were collected. The developed behavioral intervention increased adoption rates.

Keywords: *adoption; animal shelter; dog training; preference assessment*

In the present study, we experimentally assessed whether increasing certain behaviors during interactions with potential adopters influenced adoption outcomes. In Experiment 1, we validated a brief play preference assessment in order to find individual preferences for toys in shelter dogs. We found that play with specific toys in the preference assessment predicted play in more naturalistic settings (χ^2= 10.50, P < 0.001, n = 20). We then used a modification of this assessment as part of the experimental intervention. In Experiment 2, we randomly assigned dogs to the experimental structured-interaction (Group SI) and control (Group C) groups and evaluated 160 interactions between these dogs and potential adopters. The experimental intervention consisted of conducting a play preference assessment prior to the interaction and structuring the interaction once a potential adopter expressed interest in the dog. A mixed-effects logistic regression model revealed that group membership, but not morphology of the dog, was predictive of adoption outcome (χ^2= 3.95, P < 0.047). Dogs in Group SI engaged in less undesirable behavior and were 2.49 times more likely to be adopted than dogs in Group C (23.3% adopted in Group C and 39.2% adopted in Group SI). A questionnaire revealed that potential adopters did not find the structured interaction intrusive. This validated intervention could be used in animal shelters to increase adoption rates in dogs.

- P65 - BREED DIFFERENCES IN CANINE AGGRESSION - SURVEY

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Highlights:

The aim was to investigate in detail the issue of dog aggression and determine which breeds are more prone to aggression. Our survey confirmed that types of dogs categorised as "potentially dangerous breeds" or "aggressive" are in many aspects less aggressive than other breeds. Most dogs aggressive in several categories were crossbreed dogs.

Keywords: *aggression; dangerous dog; questionnaire*

In many countries were efforts to limit or even ban breeding or keeping dangerous dogs. There are many factors that play a role when assigning a "danger" level to a dog but most critics and researchers disagree as to what these factors are. Consequently, it's unfair to callously label a dog as dangerous. Nevertheless, it can't be helped that some dog breeds have more potential to cause serious harm to a person if the dog were to decide to attack.
In our study, we address the issue of dog aggression towards people and animals in Slovakia, using a questionnaire survey. We surveyed 228 respondents. Questions regarding dog aggression were divided according to two factors: Aggression towards people and Aggression towards animals. Each factor has several facets.
Our investigations resulted in an important observation that the aggression of crossbred dogs towards people was significantly higher ($p<0.001$) compared to guarding dogs, potentially dangerous breeds of dogs and stock dogs. These results confirmed that the concerns of public about increased aggression of dangerous dog breeds, sometimes referred to as "fighting breeds", are unjustified.

- P66 - DO OWNER'S GENDER INFLUENCE THE REFERENTIAL COMMUNICATION IN DOGS?

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Highlights:

We evaluated whether dogs' communicative signals were affected by owner's gender. Dogs owned by female and male owners did not differ regarding communicative abilities. The duration of gazing at the owner was similar for both groups. Likewise, the number of gaze alternation between the owner and the food was also similar for both groups.

Keywords: *dog-human communication; owner's gender; referentiality*

Studies found that dogs communicate with humans referentially and intentionally by displaying behaviors such as gazing and gaze alternation between an object of interest (food or toy) and a human partner (Miklosi et al., 2000; Savalli et al., 2014). Since Prato-Previde et al., (2006) found that women talked to their dogs significantly more than men, we hypothesized that this could also influence the way dogs communicate with female and male owners, i.e. that dogs from female owners would use more communicative behaviors than dogs from male owners.
Twenty-nine dogs (19 female owners *vs.* 10 male owners) were presented to the following procedure: a helper took the dog to the experimental room with a piece of food, she put it on one of two possible shelves (randomly chosen) that were inaccessible for the dog, and left the room. Next, the owner entered the room and remained quietly for 30 seconds standing equidistant from the two shelves. The variables recorded were: the duration that dogs gazed at the owner and the number of gaze alternation between the owner and the food. This procedure was performed three times and the median for each variable was considered in the analysis.
Both variables did not differ between dogs owned by female or male owners (Mann-Whitney test, $p>0.05$). The current exploratory study suggests that the ostensive stimulus to communicate supposedly received by dogs owned by female owners did not affect the production of communicative signals in dogs.

References

Miklósi, A., Polgárdi, R., Topál, J., Csányi, V., 2000. Intentional behaviour in dog-human communication: an experimental analysis of "showing" behaviour in the dog. Anim Cogni 3(3), 159-166.

Prato-Previde, E., Fallani, G., Valsecchi, P., 2006. Gender Differences in Owners Interacting with Pet Dogs: An Observational Study. Ethology 112, 64-73.

Savalli, C., Ades, C., Gaunet, F., 2014. Are dogs able to communicate with their owners about a desirable food in a referential and intentional way? PLOS One 9(9), e108003.

- P67 - MISINTERPRETATION OF CANINE POSTURE IN A VASE OF THE AMASIS PAINTER

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Highlights:

Attic Black Figure vases of the Amasis Painter were reviewed for images containing dogs. In works of this painter, dogs are depicted realistically in structure and pose. In at least one of these works, previous scholars have misinterpreted the behavior of the dogs. Correctly characterizing the posture of dogs on this vase influences how the images are interpreted.

Keywords: *Amasis Painter; Attic Black Figure; behavior; dog*

After centuries of neglect, the domestic dog has recently become an active area of research in the sciences and the classical world. The scenes on painted vases reflect the observed realities of everyday life in ancient Athens – including dogs. Approximately 20% of works attributed to the Amasis Painter contain at least one domestic dog, and in every case his dogs are realistic in structure and pose. None of the Amasis Painter's dogs are the famous dogs of myth (e.g. Kerberus or Argos). For these reasons, the works of the Amasis Painter seem an ideal starting point to examine the ability of canine behavior to inform vase interpretation. As a test case, I focus here on the Amasis Painter's amphora in Bloomington (71.82), where previous scholars have mischaracterized the postures and behavior of the dogs. Commentators on the Bloomington amphora have assumed that the dogs are depicted naturally, but they have misinterpreted the postures of the dogs. The dogs on this vase are alert, attentive, and playful and not, as earlier commentators have characterized them as antagonistic or aggressive. Knowing the physical state of an animal allows the observer to reasonably determine its mental and/or emotional state, which in turn, bears on the interpretation of the human actors in the scene presented on the vase.

- P68 - REASONS FOR RELINQUISHMENT OF DOGS TO THE MUNICIPAL DOG SHELTER OF ROME

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Highlights:

Dogs relinquished by owners represent a quote of shelter admissions. Literature data relate dog relinquishment causes both to dog's behavioural and sanitary traits and to owner's characteristic but no published data are available for Italy. A survey was conducted on reasons of dog relinquishment to the Municipal dog shelter of Rome in order to prevent admissions.

Keywords: *dogs; shelter; relinquishment*

A questionnaire was developed and administered to a random sample of 42 out of 479 owners in years 2005-2007 and on a sample of 38 out of 192 owners in years 2013- 2015.
Data were collected on familiar situation, experience with dogs, motivation for acquiring and provenance of the dog, reason for relinquishment (dog related =DRC or owner related =ORC) and follow up.
Data entry and analisys: Epinfo 3.5.3.
42 % of relinquishments are due to DRC, biting dogs representing 47,5% of overall DRC; among ORC (24 %) only 10 % are referred to economic problems.
Significative higher percentage (65% p 0.005) of biting dogs was observed in more recent sample and male dogs were more often aggressive (O.R.4.07 p 0.004). Unneutered animals accounted for 46,4 % of sample, 39 % were formerly adopted dogs and 42 % of owners tried reeducation before relinquishment. 48 % where still in shelter after 1 year.
Contrary to literature data the impact of dog behavioural problems was prevalent to owner's economic reasons; behavioural problems of dogs are preventable through education of dog owners and correct adoption choices . Appropriate guidelines should be developed and applied in shelters.

- P69 - PERSONALITY TRAITS THAT EMERGE IN TEN POPULAR DOG BREEDS IN ITALY

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Highlights:

The aim was to assess the relationship between canine personality scores and breeds as well as environmental factors. A Monash Canine Personality Questionnaire-Revised modified questionnaire was presented to 167 Italian dog owners. There was a significant effect of breed on Extraversion, Amicability and on Training Focus (P<0.01). Living in a house with garden versus an apartment was correlated with several personality traits.

Keywords: *breed; dog related variables; Monash Canine Personality Questionnaire-Revised; personality questionnaire*

Personality traits are influenced by both genetic and environmental factors. From the Monash Canine Personality Questionnaire-Revised (MCPQ-R), five dimensions, Extraversion, Motivation, Amicability, Training Focus and Neuroticism, were identified using 20 Italian words instead of 26, which were similar to the English words (Ley et al., 2009). The list of personality adjectives was presented to 167 Italian dog owners who rated each using a 4 point scale (breeds: German Shepherd, Golden Retriever, Cocker Spaniel, Dachschund, Pinscher, Labrador, Jack Russell, Pug, Beagle, Yorkshire Terrier). The total score per dog/trait was analyzed against factors using Kruskal Wallis and Spearman Rank Correlations (SPSS; Significance at p<0.05). There was a significant effect of breed on extraversion (W= 24.22; P<0.001; df=9, Kruskal Wallis highest score – hs: Jack Russel and Cocker Spaniel), on amicability (W= 31.52; P<0.01; df=9, hs: Golden Retriever) and on Training Focus (P<0.001; df=9, W=33.7 hs: Golden Retriever, Labrador). Pairwise comparison shows that significant difference were related to 2-3 particular breeds only for each trait. Dogs living in houses with gardens had significantly higher motivation scores (p=0.046; U= 2864; Mann Whitney), showed a strong trend towards a higher Training Focus (p=0.061, W=4069, Mann Whitney) and higher Amicability (p=0.059; W=4069) and a weak trend towards less Neuroticism (p=0.09, W=2958). This highlights the importance of environmental enrichment for dogs. Neutered or castrated dogs scored lower in Neuroticism than entire animals (p=0.047; U= 1672; Mann Whitney).
The questionnaire is a practical test for measuring differences in canine personality as rated by the dogs' owners.

References

Ley, J.M., Bennett, P.C., Coleman, G.J., 2009. A refinement and validation of the Monash Canine Personality Questionnaire (MCPQ). Appl Anim Behav Sci 116, 220–227.

- P70 - METABOLIC FACTORS, RATHER THAN NONSELECTIVE FOOD INTAKE MIGHT AFFECT OBESITY IN DOGS

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Highlights:

The performance of obesity prone and non-obesity prone dog breeds was compared in a two-way object choice test. Irrespective of their breed, dogs showed declining motivation to choose when food reward of low incentive value was used. Canine obesity may not to be related to invariable attraction to all kinds of food.

Keywords: *dog; food incentive; obesity prone breeds; two-way object choice test*

Although obesity represents a widespread problem in companion dogs, the contribution of breed-specific behavioral patterns to obesity are less investigated. In this study we compared the performance of dogs belonging to breeds that are considered more (Golden Retriever, Labrador Retriever, Beagle; N=25) or less (Border Collie, Mudi; N=23) prone to obesity. Dogs were enrolled in a two-way object choice test where they had to find hidden food following the visual cue given by the experimenter. The indicated bowl contained always food of low incentive value. In group 'empty alternative' (EA) the non-indicated bowl was empty (N=22), while in group 'reward alternative' (RA) it contained food of high incentive value (N=26). The EA group showed a decline in their motivation along the trials, as they approached the target bowls with longer latencies (P=0.022) than dogs in RA, and this effect was even more pronounced during the last three trials (P=0.001). Number of correct choices (choosing the indicated bowl) in the last three trials showed also a trend-like decline (P=0.069) in the EA group compared to RA. Obesity proneness of dog breed did not affect the latency of approach (P=0.251), nor the performance (P=0.478). Our results show that dogs, irrespectively of their breed predisposition towards developing obesity, react with declining motivation to repeated encounters with food reward of low incentive value. Based on these findings, we may draw a cautious conclusion that canine obesity is not promoted by the invariable attraction to all kinds of food.

- P71 - OWNER EVALUATIONS OF DOG PERSONALITY AND BEHAVIOUR ARE ASSOCIATED WITH BREED GROUP, BUT NOT WITH TWO OXYTOCIN RECEPTOR GENE POLYMORPHISMS

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Highlights:

Dog personality, history of aggression, and two OXTR gene SNPs were examined in 97 dogs. Owner-reported "eagerness to please" and MCPQ-R Training Focus scores varied among breed groups. MCPQ-R Amicability scores were higher in dogs with no history of aggression. No association was found between SNP genotypes and personality measures.

Keywords: *aggression; dogs; oxytocin receptor gene polymorphism; personality*

In dogs, single nucleotide polymorphisms (SNPs) in the oxytocin receptor (OXTR) gene have been associated with friendliness and human proximity-seeking (Kis et al., 2014). This behavior-gene link suggests that relationships may exist between OXTR SNPs and personality in dogs. We investigated the relationship between personality and two OXTR SNPs, rs8679684 and 19131AG, in 97 domestic dogs (47 purebred, 50 mixed). Personality was measured with the owner-reported Monash Personality Questionnaire Revised (MCPQ-R) and a questionnaire concerning dogs' history of aggression and "eagerness to please". Dog DNA was obtained via hair and buccal samples. No relationship was found between personality measures and SNP genotypes. Eagerness to please scores were positively correlated with both Training Focus (r_s = .62, p < .001) and Amicability (r_s = .41, p < .001). Amicability scores were significantly higher in dogs that had never shown aggression towards unfamiliar dogs (t(94) = -4.52, p < .001) or unfamiliar humans (t(94) = -3.34, p = .001). Herding breeds (classified as per vonHoldt et al., (2010) scored higher in eagerness to please than scent hound breeds (p = .04), and Training Focus scores of scent hounds were lower than those of herding (p = .007) and working (p = .03) breeds. The lack of relationship between these OXTR SNPs and personality in a wide sample of dogs may be due to breed-specific behavioural effects of OXTR genes.

References

Kis, A., Bence, M., Lakatos, G., Pergel, E., Turcsán, B., Pluijmakers, J., […], Kubinyi, E., 2014. Oxytocin receptor gene polymorphisms are associated with human directed social behavior in dogs (Canis familiaris). PLOS One 9, e83993.

vonHoldt, B., Pollinger, J., Lohmueller, K., Eunjung, H., Parker, H., Quignon, P., […], Wayne, R., 2010. Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. Nature 464, 898-903.

- P72 - POSITIVE AND NEGATIVE SOCIAL EXPERIENCE MODULATES SLEEP MACROSTRUCTURE IN DOGS

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Highlights:

A recently developed non-invasive polysomnography method was utilized in dogs. The effect of positive/negative social experience was examined on sleep macrostructure. After negatively valenced social stimulation dogs spent more time in REM sleep. Positively valenced stimuli resulted in longer drowsiness phase.

Keywords: *dog; polysomnography; REM sleep; stress*

Daytime events, especially emotionally valenced events and their effects on sleep physiology are well studied in humans and laboratory mammals. Duration of the rapid eye movement (REM) and slow wave sleep phase could be affected by the events during the pre-sleep period. In the present study we used a non-invasive polysomnography method in family dogs (N=16) that allow us to measure sleep macrostructure and EEG spectrum during 3-h-long sleep occasions. Before sleeping dogs were exposed to a 6 min. long emotionally positive or negative pretreatment with social stimuli in a within subject design and in balanced order. In the emotionally positive pretreatment condition dogs received petting and participated in a ball-play with the owner, while the emotionally negative preteratment was a mixture of separation, threatening approach and still face test. We found that negatively valenced stimuli caused elongated REM duration ($F_{1,30}$=19.9, $p<0.001$) and marginally a shortened latency to the first REM phase ($F_{1,30}$=3.7, $p=0.06$). After positive social experience dogs spent more time in drowsiness ($F_{1,30}$=11.24, $p=0.002$). At the same time no difference was found in slow wave sleep and total sleep efficiency between the two pretreatments. This is the first evidence that emotionally valenced stimuli affect some physiological parameters of subsequent sleep in domestic dogs.

- P73 - THE EFFECT OF OXYTOCIN ON SOCIAL RESPONSIVENESS IN A 'COOPERATIVE' AND AN 'INDEPENDENT WORKER' DOG BREED

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Highlights:

The effect of oxytocin administration and breed group on dogs' social responsiveness was investigated. Huskies and Border collies participated in three behavioural tests after intranasal administration of oxytocin or placebo. Breed groups differ in their use of gaze cues. Oxytocin administration affects differently the social behaviour of Huskies and Border collies.

Keywords: *breeds; dog (Canis familiaris); oxytocin; social responsiveness*

Dogs resemble humans not only in their human-analogue social behaviours, but also in that the oxytocin system is related to their social behaviour. Concerning the potential breed differences in the domain of social cognition, there is increasing evidence that dogs' ability to utilize human signals may vary with breed. Moreover, breeds may show differences not only in their 'inborn' communicative abilities, but also in their learning skills related to these. The aim of the present study was to explore the breed differences and the breed-specific effects of oxytocin administration on different aspects of dogs' social responsiveness. Two strikingly different breed types, cooperative workers (Border collies) and independent workers (Siberian huskies) were tested. Dogs, after having received intranasal administration of oxytocin (OT) or placebo (PL), participated an unsolvable task, social referencing test and a forced eye-contact test. We found that Border collies looked longer (χ^2=5.539, p=0.019) and sooner (χ^2=8.519, p=0.004) at their owners than Siberian huskies. After oxytocin pretreatment Border collies showed a stronger tendency to maintain eye contact with the experimenter (χ^2=7.157, p=0.007) than Siberian huskies. These results are consistent with the differential effects of human selection for social communication skills in cooperative versus independent worker breeds and suggest that neurohormonal background may have different impact on different work breeds.

- P74 - MODERATOR DOGS IN MODULATION OF CANINE BEHAVIORAL PROBLEMS

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Highlights:

Moderator dogs consist of dogs with highly specialized cognitive competence. They work in order to correct behavior of conspecifics with inadequate socialization. Investigations on behavioral and physiological measures are necessary to assess this modulation.

Keywords: *canine behavioral problems; moderator dog; socialization*

Many dog behavioural problems such as aggression, fear or anxiety are caused by hormonal modification in response to chronic stress conditions. How dogs respond to chronic stress depends on a combination of genetic and environmental factors. When organic causes of behavioural problems are excluded by clinical and hematochemical examinations, social interactions in a safe and controlled environment could be very important in helping problematic dogs.
Moderator dogs consist of dogs with highly specialised cognitive competence who work in order to correct behavior of conspecifics with inadequate socialization. Moderator dogs are adults with high intra- and inter-specific social experience who are spontaneously able to modulate heterospecific pack dynamics. Presumably they can do this because they are highly motivated to correct canine problematic behaviours, thus allowing dogs to co-operate with/or imitate activity of dog trainers. Dog trainers, with the help of moderator dogs, indicate to both species of how to communicate with each other in a correct and specific way to establish their social roles. Moderator dogs and dog trainers can modulate behaviour of other dogs in order to improve the welfare of dogs inside each inter-specific pack and during each new situation. Investigations on behavioral and physiological measures are necessary to assess animal behavior modulation that it persists over time after few sessions of interactions between a problematic dog and a moderator dog.

- P75 - COMPARING PLAYFUL AND AGGRESSIVE INTERACTIONS IN PACK-LIVING CAPTIVE WOLVES (Canis Lupus)

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Highlights:

We compared playful and aggressive social interactions of pack-living captive wolves (*Canis lupus*). All 13 wolves participated in at least one interaction. Playful bouts were longer, involved more participants and fewer onlookers than aggressive bouts. Initiators and recipients changed roles in playful, but not in aggressive interactions.

Keywords: *aggression; play; wolf (Canis lupus) social behaviour*

When playful and aggressive interactions among human children involve similar activities (e.g., chasing wrestling), it may be difficult to determine the tone of the interaction. Fry's (1987) research showed that bouts of playfighting and serious fighting among Zapotec children differed in several ways (e.g., duration, number of partners and observers, vocalizations). We extended his approach to wolves (*Canis lupus*), coding 46 social interactions from the feeding-watch video recordings of a family group of 13 (8 male, 5 female) pack-living captive wolves at the Canadian Centre for Wolf Research, Shubenacadie, NS, Canada; this pack lived in a 3.8 ha, heavily wooded enclosure and was neither socialized to humans, nor on public display. There were 27 playful and 19 aggressive interactions. All wolves participated in at least one interaction (Md = 4; range = 1 – 11). Same sex partners accounted for 41% of playful and 74% of aggressive interactions. The two juvenile wolves were not involved in aggressive interactions. Much as Fry (1987) had observed with children, playful interactions were longer than aggressive interactions, $t(31.19) = 4.10$, $p = .000$, involved more participants, $t(31.19) = 2.43$, $p = .021$, and fewer onlookers, $t(20.88) = 4.49$, $p = .000$. Initiators and recipients changed roles in playful, but not aggressive interactions, Fisher's exact probability, $p = .002$. Squeaking vocalizations were heard more often in playful interactions, while yelps were common in aggressive interactions. Differences between playful and aggressive interactions among wolves appear to be similar to those observed among children.

References

Fry, D.P., 1987. Differences between playfighting and serious fighting among Zapotec children. Ethol and Sociobiol 8, 285-306.

- P76 - DOGS' ACTIVITIES AND BEHAVIOR PROBLEMS: A COMPARISON BETWEEN ITALY AND BRAZIL

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Highlights:

An Italian and a Brazilian sample of dog owners completed a questionnaire on their dog behavior. Dogs practicing activities generally showed less behavioral problems. Agility and obedience seem to have different effects on the Italian and Brazilian dogs. Different practices in different countries are probably responsible for different outcomes.

Keywords: *activity; agility; behaviour; dog; obedience*

Dogs' wellbeing depends on filling their physical and mental needs.
A survey with 44 questions was carried out interviewing owners about dog behavior to assess if practicing activities affected the display of behavioral problems in dogs. The questionnaire was filled in by 234 Italian dog owners (IDO) and 140 Brazilian dog owners (BDO). Data was statistically analyzed using the χ^2 test ($p < 0.05$).
In the Italian sample, 40.0% of dogs did a specific activity mostly agility (22.6%) and obedience (10.7%). Italian dogs involved in agility displayed less circling ($\chi^2 = 8.160$, $p < 0.004$) and mounting ($\chi^2 = 4.340$, $p < 0.037$), but showed more fixating on objects ($\chi^2 = 6.062$, $p < 0.014$). Italian dogs who undertook obedience showed less disobeying ($\chi^2 = 5.626$, $p < 0.018$) and pulling at the leash ($\chi^2 = 4.389$, $p < 0.036$). Less BDO (24.5%) practiced activities: mostly agility (6.3%) and obedience (12.7%). BDO whose dogs were involved in agility and obedience reported less disobeying ($\chi^2 = 6.707$, $p < 0.010$; $\chi^2 = 10.809$, $p < 0.001$), pulling at the leash ($\chi^2 = 5.404$, $p < 0.020$; $X^2 = 8.410$, $p < 0.004$), and mounting ($\chi^2 = 4.174$, $p < 0.041$; $\chi^2 = 5.969$, $p < 0.015$). Brazilian dogs who did obedience showed less symptoms of separation-related problems (barking $\chi^2 = 6.138$, $p < 0.013$; chewing objects $\chi^2 = 4.992$, $p < 0.025$).
Findings suggest that activities affect dog behavior; different practices in different countries are probably responsible for different outcomes.

- P77 - COULD TIMBER WOLVES BENEFIT FROM TRAINING INTERACTIONS WITH HUMANS AS MUCH AS DOGS?

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Highlights:

We compared training in human-socialized wolves to dogs raised and kept under identical conditions. The cortisol of wolves and dogs dropped during sessions, pointing to a relaxing effect of training in both. Responses of animals varied across trainers, indicating a social component of training.

Keywords: *human-animal interactions; positive reinforcement training; stress; training; welfare*

A major source of stress for captive wild animals is the lack of control over their environment, which includes not being able to avoid human contact. Paradoxically, some studies have shown that interactions with humans may improve their welfare. We aimed to investigate the behavioral and physiological effects of the increasingly used practice of training wild animals as a means to improve handling. We evaluated training sessions with nine human-socialized individuals of a wild species, the wolf, in comparison to nine individuals of its domesticated form, the dog. All animals were raised and kept in intraspecific packs under identical conditions to control for human socialization and familiarity with training. During the sessions, the animals stayed voluntarily close to the trainers, although dogs spent more time within one meter of the trainer than wolves (99±0.2% versus 89.5±0.9%; $F = 18.658$, $p < 0.0001$). Both showed mainly behaviors related to the commands (>90% of the time), indicating concentration to the task. The salivary cortisol of wolves and dogs dropped during the sessions ($F = 8.204$, $p = 0.004$), pointing to a similar stress-reducing effect of the training in both. Behavioral parameters and cortisol levels of wolves and dogs varied across trainers (ranging from 5.3% to 22.8% of variability), which indicates the anti-stress effect of training has a social component, aside of the rewarding effect of getting food and control over the situation. Our results support the use of training as a potentially powerful tool for improving the welfare of captive wild animals.

- P78 - ITALIAN POINTING DOGS AND THE OTHER POINTING DOG BREEDS: ARE THERE BEHAVIORAL DIFFERENCES?

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Highlights:

Behavioral differences between Italian Pointing Dogs and the Other Pointing Dogs were investigated. An online survey including the C-BARQ collected 156 questionnaires. Dogs belonging to group 7 are similar from a behavioral point of view. Italian pointing dogs showed more separation-related behaviors than other pointing breeds.

Keywords: *behavior; breed; C-BARQ; Italian pointing dog; separation-related behavior*

According to the Fédération Cynologique Internationale's nomenclature, all pointing dogs are clustered together into group 7. The aim of this study was to assess if there are behavioral differences between Italian pointing dogs (IPD) and other pointing dog breeds (OPD) belonging to group 7. An online survey was carried out. The questionnaire included information about owner's data, dog's data, and dog's management, together with the Italian version of the Canine Behavioural Assessment and Research Questionnaire[(100)] (C-BARQ). Eighty owners of IPD and 76 owners of OPD filled in the questionnaire. The two groups were balanced for dogs' sex, age and housing conditions. Following the C-BARQ scoring method, the answers provided by owners were transformed in scores for 14 categories of canine behavior: stranger, owner and dog directed aggression; dog rivalry; non-social fear; stranger and dog directed fear; touch sensitivity; separation-related behavior; attachment/ attention-seeking; trainability; chasing; excitability; energy level. The Mann-Whitney U test ($p < 0.05$) was used to compare the scores of the two groups for each category.
The only statistically significant difference was found for separation-related behaviors, whose scores resulted higher for IPD than for OPD ($U = 2120.5$, $p = 0.048$).
Results suggest that dogs belonging to group 7 are very similar from a behavioral point of view. However, Italian pointing dogs seem to be more prone to show separation-related problems. Owners and behaviorists should be aware of such predispositions, in order to effectively prevent and treat it.

- P79 - DOGS' RESPONSES TO DIFFERENT APPROACH MODALITIES PERFORMED BY A MALE STRANGER

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Highlights:

Twenty-five dogs were tested to evaluate responses to different approaches by unfamiliar men. Type of response and stress signals were recorded during an indirect and a direct approach. Dogs responded in a more friendly way to the indirect approach. Dogs tended to display more stress signals in the direct approach.

Keywords: *approach; dog; dog-human communication; stress signals*

The study of dogs' responses to an approaching human plays an important role both for the development of a better human-dog relationship and for dog training. The aim of this study was to assess the dog response to different approach modalities. Twenty-five dogs of different breeds or mixed-breed, 17 females and 8 males, 56.4±26.2 months old, underwent a behavioral test where a male stranger (MS) approached the subject using two different modalities. In the indirect approach (IA), the MS approached the dog with a semicircle walk avoiding eye contact and stood at the side of the dog for 10 seconds; in the direct approach (DA) MS walked in a straight line staring at the dog and stood in front of the dog for 10 seconds. The test execution order was randomized. Dogs' responses were scored 1 to 6 as follows: aggressive (1), active avoidant, passive avoidant, ambivalent, passive, or friendly (6). In addition, the duration of five stress signals (nose licking, paw lifting, yawning, blinking, shaking) was measured and summed. The statistical analysis was performed using Wilcoxon test ($p < 0.05$). Dogs responded more friendly to IA than to DA (median: 6.0 versus 6.0, $p = 0.021$). Dogs showed a tendency to display stress signals more in DA than in IA (median: 1.0 versus 0.0, $p = 0.201$). A direct approach seem to be more stressful for dogs, likely because it is perceived as more threatening. This study helps understanding the role of human posture in human-dog communication.

- P80 - DO ALL PACK-HUNTING CANIDS NEED TO BE LARGE AND HYPERCARNIVOROUS?

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Highlights:

The ancestral reconstruction of relations between hypercarnivorous adaptation, body size and cooperative hunting was performed within 94 species of Canidae (including fossil representatives). There is no distinctive linkage between occurrence of cooperative hunting and larger body size. Hypercarnivorous canid is just a special case of cooperative hunter in Caninae.

Keywords: *body size; Canidae; hypercarnivory; pack-hunting*

Social living is very useful in the way of anti-predator strategy and also effective hunting. According to Carbone´s rule, there is a noticeable transition from feeding on small prey to large prey (equal or larger than predator), occurring at predator mass 21,5 kg. In principal, hunting of larger prey is more effective in group for canids. Animals hunting prey larger than themselves have specific dental adaptations. This complex of hypercarnivorous traits was proposed as a possible indicator of pack hunting. To explain the consequences of the origin of canid social behavior, we reconstructed evolution of cooperative hunting on complete phylogeny of the Canidae (94 species), including fossil ones. The enlargement of paracones relative to metacones on the first two upper molars were identified as the best osteological correlates of cooperative hunting and analyzed together with body size and the best osteological indicators of hypercarnivory (fully trenchant talonid on the first lower molar and small hypocone on the first upper molar) in programme Mesquite. Our results did not show any obvious relation between occurrence of cooperative hunting and larger body size. This is probably relate to environmental circumstances (vast arid grasslands), where hunting in group was more advantageous for all canids, not only the larger ones. Hypercarnivory occurred in some species smaller than 20 kg and consequently, not all large canids had adaptations for hypercarnivory. Then, it is obvious that hypercarnivorous canid is only special case of cooperative hunter in Caninae as a consequence of food supply changes (large-bodied herbivores).

- P81 - NASAL OXYTOCIN ADMINISTRATION ENHANCES GAZING AT EYES OF SMILING HUMANS IN DOMESTIC DOGS – PRELIMINARY RESULTS

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Highlights:

The study explored how nasal oxytocin administration affects to the face processing of domestic dogs. The looking patterns of dogs were tracked during viewing of photographs of human emotional faces. The results showed that oxytocin treatment enhanced attention to eye region of smiling humans. In addition, oxytocin treatment weakened attention allocation to eyes of threatening faces.

Keywords: *eye-gaze; eye tracking; face processing; oxytocin*

The neuropeptide oxytocin has a critical role in perception of social cues. Here, we investigated how oxytocin affects the processing of human emotional faces by dogs. Eye tracking was used to assess looking patterns of 42 dogs (31 females, 11 males; average age 5.1 years) while viewing pictures of human male faces displaying smiling or angry expression. Approximately 46 minutes prior the test the dogs were treated with oxytocin (OXT; Syntocinon® 40 IU/ml, Novartis) or a placebo (PLB; Naso NaCl 0,9 %, Ratiopharm) nasal spray. The test was repeated on another day with cross-over design. We found that after the OXT treatment dogs made more fixations at the eyes of smiling faces (Md 3.0 ± QD 2.6 vs. 2.5 ± 1.75; Wilcoxon Z = -1.98; p = 0.048) and revisited the eyes of smiling faces more often (1.5 ± 1.0 vs. 1.0 ± 0.8; Z = -2.69; p = 0.007) than after the PLB treatment. Moreover, after the PLB treatment dogs revisited the eyes of angry faces more often than the eyes of the smiling faces (1.5 ± 1.5 vs. 1.0 ± 0.8; Z = -2.06; p = 0.040), but after the OXT treatments such discrimination could not be detected (1.0 ± 1.5 vs. 1.5 ± 1.0; Z = -0.36; p = 0.716). Taken together, oxytocin has the potential to increase visual attention to positive emotion related eye-gaze cues in dogs and in turn it reduces attention allocation to threatening signals, which may facilitate the communication between humans and dogs.

- P82 - MOTOR LATERALITY IN DOMESTIC DOGS: DOES THE FAMILIARITY WITH THE HANDLER INFLUENCE THE PAW PREFERENCE?

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Highlights:

Laterality is recognized in many animal species and known to be task-dependent. Thirty-eight dogs were tested in the First-stepping test with the owner and an unfamiliar handler. Paw preference resulting from the two tests showed a low concordance. Familiarity with the handler may influence paw preference assessment.

Keywords: *dog; familiarity; first-stepping test; handler; laterality*

The term laterality refers to the preference most mammals show for one body side over the other. The aim of this study was to evaluate the reproducibility of the First-stepping test (Tomkins et al., 2010) in relation to the familiarity with the handler. Thirty-eight adult dogs (22 females, 16 males, different breeds) were tested twice in a modified version of Tomkins' test (30 repetitions instead of 50), once with the owner and once with an unfamiliar handler, one day apart.
The paw preference (PP) for each dog in both tests was determined as suggested by Tomkins et al. (2010), calculating the lateralization index and considering a significant preference for Z-scores < -1.96 (left PP) or $> +1.96$ (right PP).
There was a low concordance between the Z-scores of the two tests (Cohens' Kappa coefficient = 0.44). In detail, the Z-score of 14 dogs was different in relation to the familiarity with the handler: 1 dog showed a right PP with the owner and a left PP with the unfamiliar handler; 9 dogs showed a non-significant Z-score with the owner and a significant Z-score with the unfamiliar handler; 4 dogs showed a significant Z-score with the owner and a non-significant Z-score with the unfamiliar handler.
Previous literature on dogs and other mammals reports that laterality is strongly task-dependent. The current findings suggest that PP may be influenced by other factors, such as the familiarity with the handler, which should be taken into account when testing animals for motor laterality.

References

Tomkins, L.M., Thomson, P.C., McGreevy, P.D., 2010. First-stepping Test as a measure of motor laterality in dogs (*Canis familiaris*). J Vet Behav Clin Applic Res 5, 247-255.

- P83 - DOES SOCIO-ECOLOGY DRIVE DIFFERENCES BETWEEN WOLVES AND DOG IN ALERTNESS DURING REST/SLEEP?

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Highlights:

Alertness is an indicator for the state of activation on the sleep-wake axis. We compared alertness of wolves and dogs in two different situations: (1) resting (i.e. sleeping) and (2) awake, but inactive. Wolves were less alert than dogs in both conditions, probably caused by the socio-ecological differences between wolves and dogs due to domestication.

Keywords: *alertness; domestic dog; sleep; socio-ecology; wolf*

Interspecific variation in sleep might be driven by the adaptations of animals towards their ecological niche and life style. By comparing wolves *(Canis lupus)* and dogs *(Canis lupus familiaris)* we might provide some new insights into how much differences in sleep/rest patterns are driven by socio-ecological needs. Although wolves are the closest living relatives of dogs, they occupy different socio-ecological niches. Because dogs mainly live in human-shaped environments, they are potentially less at risk from natural threats than wolves. Hence, we hypothesized that alertness – an indicator for the state of activation on the sleep-wake axis – might be greater in wolves than in dogs. We compared cardiac output – measured by the Polar RS800CX heart rate (HR) monitor – of six similarly raised and kept pack-living wolves and dogs in two different behavioural conditions: (1) resting (i.e. sleeping) and (2) awake, but inactive. In contrast to our expectations, the wolves showed significantly lower HRs than the dogs ($F_{1,13}$=6.60, p=0.024) both when they were awake/not active as well as when they were resting/sleeping ($F_{1,27}$=20.97, p<0.001). Also, heart rate variability (RMSSD) of the wolves was significantly higher than that of the dogs ($F_{1,37}$=4.79, p=0.035) in both conditions ($F_{1,37}$=26.56, p<0.001), indicating a greater relaxation of the wolves during rest/sleep. We propose that the dependency of dogs on humans and, therefore, their potentially less predictive social and ecological environment as compared to wolves, might have caused the dogs' greater basic alertness.

- P84 - DIVERSIFYING SELECTION BETWEEN FREE-BREEDING AND PURE-BREED DOGS AT A FUNCTIONAL GENE

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Highlights:

Different selection pressures on free-breeding and domestic dogs affect immunity genes. Comparison of DNA sequence for MARCH7 gene between pure-breed dogs, free-breeding dogs and wolves. Preliminary analysis found SNP insertion mutation discovered in domestic dog samples.

Keywords: *diversifying selection; free-breeding dogs; MARCH7 gene; pure-breed dogs*

Free-breeding and pure-breed dogs form distinct genetic populations, although not entirely isolated. In pure-breed dogs, artificial selection for specific phenotypic traits may lead to relaxed selection pressures on traits important for independent survival, traits related to mate choice and reproduction, disease resistance and immunity. In contrast, free-breeding dogs are subject to natural selection similar as wild canids. Differences in the strength of natural and artificial selection between these groups may have important implications for health of individuals.

This study is focused on MARCH7 gene (Membrane-Associated Ring Finger, where an intronic SNP mutation has been shown to occur in different frequencies in pure-breed and free-breeding dogs. MARCH7 is involved in regulation of neuronal stem cells, T lymphocytes and immune tolerance.

We analyse DNA sequence data for MARCH7 gene between pure-breed and free-breeding dogs, using samples from grey wolves to infer ancestral state. Preliminary analysis has revealed mutations present in pure-breed dog samples. An A/T mutation has been found in the intronic region of MARCH7, 15 base pairs before an exon. The derived A allele has been detected in a heterozygous state in four individuals tested, while other individuals were homozygous for the T allele. Further sequencing of these genes in free-ranging dog and wolf samples will be conducted with the aim to assess whether there are differences in allele frequencies between these groups. Comparison of sequences between these groups will allow us to assess whether MARCH 7 gene is under diversifying selection.

- P85 - COMMUNICATION OR NOISE POLLUTION? ROLE OF THE ACOUSTIC FEATURES OF DOG BARKING IN THE AUDITORY NUISANCE

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Highlights:

A test about the communicative relevance of auditory nuisance in dog barking. Playback test for evaluating the annoying effect of dog barking and the attributed inner states. Acoustic features that were selected for effective vocal signaling may be annoying for humans.

Keywords: *bioacoustics; communication; dog; nuisance bark*

Excessive dog barking is among the leading sources of noise pollution world-wide; however, the biological causation of barking annoyance remained uninvestigated. Previous research proved that human listeners can predict the barking's context and the inner state of the dog based on the acoustic parameters of the dog bark. Our questions were: is the nuisance rating affected by the acoustic parameters of barks; does the attributed inner state of the dog and the nuisance caused by its barks correlate; does the gender and country of origin affect the subjects' sensitivity to barking. Participants from Hungary (N=100) and Brazil (N=60) were tested with sets of 27 artificial bark sequences. Subjects rated each bark according to the inner state of the dog and the nuisance caused by the particular bark. Subjects from both countries found high-pitched barks the most annoying and also harsh, fast-pulsing, low-pitched barks. Men found the high-pitched barks more annoying than the women did ($F(1,4300)=7.838$; $p=0.005$; mean annoyance ratings: females: 31.94±27.97; males: 39.14±26.84). Nuisance ratings showed positive correlation with assumed negative inner states of the dog ($\rho_f=0.69$; $\rho_d=0.691$; $P<0,001$), positive emotional ratings showed negative correlation with the nuisance level ($\rho_h=-0.694$; $\rho_p=-0.599$; $P<0,001$). Using dog barks as a model, we concluded that vocalizations with emotionally intense, negative valence can annoy humans. Compare our results with previous studies this nuisance effect can be connected to some of the social contexts and inner-states of the dog, where barking can be adaptive from the evolutionary aspect, by recruiting the attention of the owner.

- P86 - DO YOU BELIEVE IN DOG: EXPLORING NON-TRADITIONAL SCIENCE COMMUNICATION PLATFORMS

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Highlights:

Most people who own and work with dogs do not access scientific literature. A non-traditional science communication platform was established to share canine science. Over 140 canine science articles have been accessed by an engaged global audience. Motivating agents, successes and challenges associated with non-traditional science communication platforms are reported.

Keywords: *canine science; public engagement; science communication; social media*

Science communication was traditionally performed by mainstream journalists translating complex scientific findings to make them accessible to general audiences. Today, direct exchanges between researchers, scientific institutions and the general public are increasingly common using digital media platforms. Despite the numerous welfare implications of canine science, most people who own and work with dogs do not access scientific literature. As a result, scientist participation in outreach communication could be notably relevant to canine science. 'Do You Believe in Dog' is a blog with associated social media presence, created in 2012. The aim was to create a platform for outreach, with the goal of improving awareness and public engagement with the field of canine science. The platform has shared synopses of research findings, researchers' personal journeys, the process and challenges of canine science. More recently, it serves as a platform for other canine researchers (n = 14) to present and discuss their research directly with an established and engaged general audience. Over 140 articles have been posted on the blog attracting over 366,250 site hits. The most popular post has been viewed more than 13,800 times. The blog is accessed globally, with the majority of readers originating from the USA, Russia, France, Australia, UK, Canada and Germany. The main referral sites to the blog are Google, Facebook and Twitter. The motivating agents as to why researchers take on these forms of engagement, along with key successes and challenges of this collaborative endeavor will be reported.

- P87 - WHAT'S IN A NAME? UNDERSTANDING THE POWER OF BREED LABELS IN ANIMAL SHELTERS

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Highlights:

The pit-bull-type dog was perceived more negatively than photographs of other breeds. Length of stay was longer for pit-bull-type dogs than similar looking dogs with other breed labels. In videos, perceptions of attractiveness were altered when dogs were breed labeled or unlabeled. Removing breed labels increased adoptions and reduced length of stay for all breed groups.

Keywords: *adoption; animal shelter; breed; dog; length of stay*

Previous research has indicated that certain breeds of dogs stay longer in shelters than others. However, exactly how breed perception and identification influence potential adopters' decisions remains unclear. In Study 1, the perceived behavioral and adoptability characteristics of a pit-bull-type dog were compared with those of a Labrador Retriever and a Border Collie. In Study 2, lengths of stay and perceived attractiveness of dogs that were labeled as pit-bull-type breeds were compared to dogs that were phenotypically similar but were labeled as another breed at an animal shelter. We called the latter dogs "lookalikes." In Study 3, we compared perceived attractiveness in video recordings of pit-bull-type dogs and lookalikes with and without breed labels. Lastly, data from an animal shelter that ceased applying breed labeling on kennels were analyzed, and lengths of stay and outcomes for all dog breeds, including pit bulls, before and after the change in labeling practice were compared. We found that, when presented unlabeled, pit-bull-type dogs were just as attractive to adopters as lookalikes, but attractiveness of the same dogs was significantly reduced when breed labels were presented. Data from the shelter that removed breed labels showed that this is a low-cost strategy that can improve outcomes for all dogs in animal shelters.

- P88 - DOGS OBEY BETTER TO GESTURAL THAN VOCAL STIMULI BY STRANGERS

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Highlights:

In dog-human communication both gestures and verbal information are important for dogs. Gestural vs. vocal discriminative stimuli are given to fifteen dogs by their owner and a stranger. Results show that in dogs the gestural discriminative stimuli are independent from the cue-giver. The vocal message is less effective when provided by a stranger.

Keywords: gestural stimuli; human-dog familiarity; incongruent information; training; vocal stimuli

When communicating with dogs, humans often combine verbal and gestural cues. Here we compared the relative relevance of gestural versus verbal stimuli in relation with the familiarity of the cue-giver. Fifteen water rescue dogs were asked to perform four actions (SIT, LIE DOWN, STAY and COME), by providing them only *gestural*, only *verbal* and *contrasting* stimuli (i.e. a gestural and a verbal stimulus indicating different actions). Each dog underwent the procedure twice, once with the owner and once with a stranger providing stimuli. Dogs' responses to the presented stimuli were collected as a binomial variable (expressed / did not express the requested behavior); for the contrasting condition response to the gestural stimulus was arbitrarily considered as the requested one. When stimuli were provided by the owner, the highest probability of observing the requested behavior was observed in the gestural than vocal ($P=0.020$; adjusted P after Generalized Estimation Equations model) or contrasting ($P<0.001$) conditions; the lowest probability was observed in the vocal condition (vs. contrasting: $P<0.001$). With the stranger, the vocal condition showed a lower probability than the gestural ($P<0.001$) and contrasting ($P=0.01$) conditions. The probability of expressing the requested behavior was higher if the owner provided stimuli than if the stranger provided stimuli in the vocal ($P<0.001$) and contrasting conditions ($P<0.001$). Conclusion: the gestures of the handler and the stranger were both equally effective on dog responses, whereas vocal stimuli were more difficult to generalize.

- P89 - SEX DIFFERENCES IN THE ACQUISITION OF SPATIAL INFORMATION FROM HUMAN DEMONSTRATORS BY DOGS

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Highlights:

Dogs underwent a deferred imitation task with conflicting allo- and ego-centric information. All dogs used preferentially an allocentric strategy to solve the task. Males were quicker in resorting to an egocentric strategy when allocentric became unsuitable.

Keywords: *deferred imitation; dog; flexibility; sex spatial strategy*

In deferred imitation tasks, dogs typically act in the location, rather than on the object, where the demonstrator acted. However it is not known what kind of spatial information (allocentric or egocentric) dogs use to encode and recall the location of the demonstration and whether this differs between sexes.
We tested 15 dogs (8 females, 7 males), previously trained with the Do as I Do method (Fugazza & Miklósi, 2014), in a deferred imitation task. A human demonstrator approached one of two identical targets, at two different locations; after a short interval, the dog was required to imitate the action, facing a direction opposite to that faced during the demonstration, thereby with conflicting allocentric and egocentric information. We used the number of allocentric or egocentric choices in 6 trials to classify dogs as egocentric or allocentric. Subsequently dogs were tested on their ability to resort to the non-preferred strategy.
Dogs preferentially used an allocentric strategy in the first phase (median allocentric choices = 5, min = 5, max = 6); when such strategy became unsuitable to solve the task, males outperformed females, reaching the set criterion of 3 egocentric choices in a row in fewer trials (median trials to criterion: males = 3, females = 9, Mann-Whitney U Test P = 0.04). Results demonstrate a general preference by dogs for acquiring allocentric information from humans. The higher flexibility shown by males supports the existence of sex-related differences in spatial cognition in dogs, as observed in other species (Rodriguez at al., 2010).

References

Fugazza, C., Miklósi, Á., 2013. Deferred imitation and declarative memory in dogs. Anim Cogn 17(2), 237-247.

Rodriguez, C.A., Torres, A., Mackintosh, N.J., Chamizo, V.D., 2010. Sex differences in the strategies used by rats to solve a navigation task. Journal of Experimental Psychology: Anim Behav Proc 36, 395-401.

- P90 - DOGS' TV WATCHING BEHAVIOR MAY PREDICT THEIR COMMUNICATION ABILITY WITH HUMAN: MORE POODLES WATCH TV THAN CHIHUAHUAS OR MINIATURE DACHSHUNDS

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Highlights:

Surveys to 320 pet dog owners in Japan revealed breed differences in their TV watching behavior. Dogs participating in animal assisted therapy showed higher rate of TV watching compared to non-therapy dogs. While half of toy poodles watched TV, almost no Chihuahuas did. DNA analysis is underway.

Keywords: *breed differences; genetics; predictability; therapy dogs; TV watching behavior*

In the process of conducting visual discrimination tasks with dogs we have noted that those, which are good at the visual discrimination task tend to watch TV at home. We then conducted surveys to 320 pet dog owners about their pet's TV watching behavior. Results show 20 % of them watch TV. Some dogs strongly react to what is on TV while others completely ignore or pay no attention to what is on. Dogs' reaction included barking at the TV, staring at what is on, scratching, or following the animal to the back of the TV. These reactions indicate that dogs understand what is on TV and keep their eyes on it. In some homes, one of them watches and others don't, suggesting that environment is not the sole factor determining the TV watching behavior. We found some breed differences as well. Toy poodles are the most common breed in Japan followed by Chihuahuas and miniature dachshund. Our results show that 52% of the poodles watch TV while much 14% and 11% for Chihuahuas and Miniature dachshunds respectively($p<.01$). While less than 20% of non-therapy dogs watched TV, 60% of therapy dogs watched TV ($\chi^2=23.614$ $p<.01$). Buccal smears of toy poodles were collected from 20 toy poodles (10 TV watcher and 10 non-watcher). Samples were analyzed for dopamine receptor but so far, no differences among them in genotype or allele frequency were found.
Data with therapy dogs suggest that TV watching behavior is related to good human-dog communication ability of the dogs living at home.

- P91 - THE ROLE OF PREVIOUS EXPERIENCES WITH HUMANS IN INHIBITORY CONTROL OF DOMESTIC DOGS (Canis Familiaris)

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Highlights:

Shelter dogs showed a poorer performance in the A-not-B task compared to pet dogs but no differences in the cylinder task were observed. Previous experiences with humans during ontogeny would affect the inhibitory control of dogs.

Keywords: *A-not-B; cylinder task; inhibitory control; learning; shelter dogs*

Inhibitory control is a complex construct that can be broadly defined as the ability to resist the urge to do something that is immediately tempting, but ultimately harmful or counterproductive. Our first aim was to evaluate the importance of learning and ontogeny in performing inhibitory tasks. Also, we assessed whether there is a correlation between both tasks by comparing performance in the same subjects. To accomplish these objectives we assessed two groups of dogs with different levels of social interaction with humans, shelter and pet dogs, in two inhibitory control tasks. 1) In the *A-not-B task*, dogs have to resist searching for food in a previously rewarded location, and 2) in the *cylinder task*, dogs were required to resist approaching visible food directly in favor of a detour reaching response. Results showed that shelter dogs had a significantly poorer performance in the A-not-B task, compared with pet dogs. However, no differences were observed in the cylinder task. The poorer performance of shelter dogs might be related to their scarce human contact in everyday life, which reduces the opportunities to learn to inhibit certain responses. This result would highlight the importance of ontogeny in developing this ability. On the other hand, no correlations were found between both tasks, which would contribute to the debate about the context specificity of inhibitory control in dogs.

- P92 - RELATIONSHIP BETWEEN TEMPERAMENT AND VULNERABILITY TO DISEASES IN SHELTER DOGS

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Highlights:

A procedure to assess dog temperament was applied to 28 shelter dogs, captured as stray. Blood samples were collected from each dog twice, in order to evaluate their immunological state. Dogs were monitored for one month to detect eventual symptoms of disease. Bold dogs seem to cope better than shy with stress: most of them did not get any disease.

Keywords: *dogs; shelter; temperament; vulnerability to diseases*

In vertebrate species, personalities vary along an axis the extremes of which are represented by individuals 'bold' and 'shy'. Bold individuals are more aggressive and dominant, facing new contexts and situations quicker than shies, even if less prone to innovate. Shy ones are more passive, with a low speed of exploration although more thoroughly. Furthermore, shy individuals have a higher activity of HPA axis making them more vulnerable to stress related diseases.
This study aims to verify the relationship between temperament and disease vulnerability in domestic dogs (*Canis familiaris*), coping a stressful event such as entering in a dog shelter.
Behavioural observations, the Novel Object and a T-maze tests were utilized to evaluate the temperament of 28 dogs, captured as stray. A blood sample from each dog was taken at the entrance in the shelter and after a month of permanence, to verify and monitor their immunological state.
An index built on a PCA on dog behavior, related to the results of the tests mentioned, ordered the 28 dogs on the base of their boldness-shyness.
The first 10 but one (the 6th) dogs showed either an improved or a stable health status, both in term of absence of disease symptoms and immunological parameters. The 34,71% of dogs had a worsening of their health status and they were from the 11th to the 28th dog; the pattern was quite mixed, but there was a prevalence of health status worsening among the shiest dogs.
Confirming what it has been found in other species of vertebrates, the results of this research seem to confirm that bold and shy dog vulnerability to diseases might be different especially when they have to cope with a stressful and loaded of infecting pressure environment, such as a dog shelter.

- P93 - WHAT EYE-TRACKING REVEALS ABOUT DOG'S PERCEPTION AND UNDERSTANDING OF HUMANS

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Highlights:

We conducted eye-tracking studies to investigate the perception of human faces by pet and lab dogs. The results revealed differences of looking at emotional human faces between pet and lab dogs. Both pet and lab dogs showed a strong left gaze bias. These findings add further evidence for the high sensitivity of dogs for perceiving humans.

Keywords: *emotion; eye-tracking; face; left-gaze-bias; perception*

Our understanding of dogs' behavior includes what dogs understand about us. Several studies have examined how dogs 'read' human faces. For instance, dogs can discriminate familiar faces by active choice (Huber et al., 2013). They can do so by using the internal facial features only, although showing a tendency for configural elaboration (Pitteri et al., 2014). Furthermore, dogs can discriminate between human faces showing different emotional expressions (Müller et al., 2015) and can integrate bimodal sensory emotional information to do so (Albuquerque et al., 2016). Here we present the results of an eye-tracking study that aimed to investigate the processing of the human face by dogs. We examined how dogs from two different living environments and varying experience with humans, pet and lab dogs, scan familiar and unfamiliar human faces expressing four different emotions (Barber et al., *submitted*). The results revealed pronounced differences between pet and lab dogs. For instance, the lab dogs spent more time fixating the picture than the pet dogs (LMM: $F_{1,19.6}$=7.27, p=0.014), and more time looking at the positive compared to the negative emotions ($F_{1, 473.6}$=4.35, p=0.04). These findings suggest an influence of the amount of exposure to humans on face processing in dogs. In addition, for both types of dogs there was strong evidence of a left gaze bias, with 92.5% of the first fixations being directed towards the right side of the face (GLMM: estimate=2.69 +/- 0.19, z=14.12, p<0.001). These findings add further evidence for the high sensitivity of dogs to human faces.

References

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., Mills, D., 2016. Dogs recognize dog and human emotions. Biology Letters 12(1), 20150883.

Barber, A., Müller, C.A., Randi, D., Huber, L. .The processing of human emotional faces by pet and lab dogs: evidence for lateralization and experience effects. *Submitted*

Huber, L., Racca, A., Scaf, B., Virányi, Z., Range, F., 2013. Discrimination of familiar human faces in dogs (Canis familiaris). Learning and Motivation 44(4), 258-269.

Müller, C.A., Schmitt, K., Barber, A.L.A., Huber, L., 2015. Dogs Can Discriminate Emotional Expressions of Human Faces. Current Biology 25, 1-5.

Pitteri, E., Mongillo, P., Carnier, P., Marinelli, L., Huber, L., 2014. Part-based and configural processing of owner's face in dogs. PLOS One 9(9), e108176.

- P94 - THE NEED FOR SOCIALIZATION OF CAPTIVE WOLVES: UNDERSTANDING HUMAN-ANIMAL RELATIONSHIPS

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Highlights:

Habituation, taming, socialization, imprinting, and domestication are widely misunderstood concepts. Yet, they differ significantly in the essence of human-animal relationship and animal welfare. Wolves are animals who need to be socialized to reach the highest possible welfare in captivity. A more sufficient conceptualization in the field of human-animal relationships is developed.

Keywords: *animal behavior; animal welfare; human–animal relationships; inter-specific communication; umwelt theory*

Due to their genetically inherited fear of humans, captive wolves are notorious for persistent escape attempts, self-destructive behaviours, stereotypies and over-all suffering. Socialization of wolves with humans makes the animals more suitable for life in captivity by reducing their fear of humans. Unfortunately, the methods of socialization are still widely unknown and its advantages over habituation or taming remain misunderstood. This interdisciplinary study (combining zoology, animal welfare studies, ethology, comparative psychology, etc.) explains the proper methodology of socialization for animal welfare purposes. A semiotic approach (predominantly the Umwelt theory) is used to understand the changes in the animal's Umwelt and human–animal relationship. The theoretical contribution is supported by the author's experience working with socialized wolves and various other species with different human-animal relationships in USA, Germany, Norway and Thailand. The study shows how proper socialization aims to change the human's significance in the animal's Umwelt into social partner. This requires social human-imprinting, and using positive taming methods. In fact, aversive techniques, e.g. dominance theory and punishment, are counter-productive. Working "on animal terms" and establishing effective inter-specific communication is crucial for maintaining cooperative relationships. Furthermore, socialized wolves have a higher welfare in captivity than their tamed or merely habituated conspecifics. The author concludes that considering the human-animal relationship and the treatment practices it requires, improves our understanding of captive animal welfare, animal behaviour and human-animal communication. The author further suggests that a zoosemiotic approach complements more mainstream ethological knowledge in human–animal interactions and is capable of advancing animal welfare.

- P95 - THE RANDAGIAMOTM PROGRAM INCREASES SOCIABILITY IN SHELTER'S DOGS

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Highlights:

RandAgiamo™ is a project aimed to increase adoptability of shelter dogs in Italy. This study assessed the effect of its standard training and socialization protocol on dogs' behavior. The application of the RandAgiamo™ protocol increased the *Sociability* of the dogs over the time. Sociable dogs are more likely to perform better in exercises.

Keywords: *dog; shelter; sociability; training*

Sociability is one of the most attractive characteristics for the adoption of shelter's dogs. RandAgiamo™ is a project implemented in a rescue shelter in central Italy (Perugia) (Menchetti et al., 2015). It is aimed to increase dogs' adoption rate, promote welfare through environmental and social enrichment, and facilitate relationships with new adoptive families. A group of 15 dogs was selected by the criteria of an Adoptability Index Score (IDA) (Catalani, 2007). Then, they were submitted to a standardized training and socialization protocol, consisting in six sessions (T1-T6), each one including a series of ten exercises. At each session dogs were behaviorally assessed by a 5 Likert score system, measuring the following predefined behavioral characteristic: *apathy, diffidence, fear, sociability, confidence, excitement, competitiveness* and *aggression*. A 4-point scale assessed the dogs' performance of each exercise. Data were analyzed by GEE using cumulative logit function. *Sociability* was related to size (Wald χ^2=28.6, p<0.001), age (Wald χ^2=11.5, p<0.01), gender (Wald χ^2=49.6, p<0.001), and length of stay (Wald χ^2=14.7, p<0.001) of dogs as well as to exercise (Wald χ^2=10786.4, p<0.001). *Sociability* increased from T1 to T6 (Wald χ^2=100.4, p<0.001; OR=2.1, 95% CI=1.6, 2.8). Dogs ranking higher in *sociability* were more likely to achieve high performance scores (Wald χ^2=55.3, p<0.001; OR=3.4, 95% CI=2.4, 4.6). The RandAgiamo™ protocol influenced some behavioral characteristics of shelter's dogs increasing their *sociability*. This change improves dog's performance and could contribute to promote shelter dogs' adoption rate and satisfaction of adopters.

Index of Authors

Index of Keywords

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